

THE PROCEEDINGS OF THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Series A. GENERAL ENTOMOLOGY

World List abbreviation: *Proc. R. ent. Soc. Lond.* (A)

CONTENTS

	PAGE
FORD, E. B., M.A., B.Sc., F.R.E.S. Studies on the chemistry of pigments in the Lepidoptera, with reference to their bearing on systematics. 1. The anthoxanthins . . .	65-90
HINTON, H. E., Ph.D., F.R.E.S. The larva and pupa of <i>Tachinus subterraneus</i> (Linnaeus) (Coleoptera, STAPHYLINIDAE) . . .	93-98, 15 figs.
REID, J. A., B.Sc., A.R.C.S., F.R.E.S. A note on oviposition preferences in <i>Smerinthus populi</i> (L.) (Lepidoptera, SPHINGIDAE) . . .	91-92
BOOK NOTICES	90, 99-100

LONDON:

PUBLISHED BY THE SOCIETY AND

SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 9s. 0d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1941–1942.

K. G. BLAIR, D.Sc., *President*.

PROF. P. A. BUXTON, M.A.
G. FOX-WILSON, N.D.H.
HUGH MAIN, B.Sc. } *Vice-Presidents*.

BRIGADIER W. H. EVANS, C.S.I., C.I.E., D.S.O., *Treasurer*.

N. D. RILEY, *Secretary*.

F. J. GRIFFIN, A.L.A., *Registrar*.

Other Members of Council.

PROF. H. G. CHAMPION, C.I.E., M.A.
E. A. COCKAYNE, M.A., M.D., F.R.C.P.
A. S. CORBET, D.Sc., Ph.D., F.I.C.
COL. F. A. LABOUCHERE.
A. M. MASSEE, D.Sc.
C. POTTER, B.Sc., Ph.D.

O. W. RICHARDS, M.A., D.Sc.
THE HON. MIRIAM ROTHSCHILD.
J. SMART, B.Sc., Ph.D.
W. H. T. TAMS.
A. WELTI.

Finance and House Committee.

A. WELTI (Chairman).

H. M. EDELSTEN.
A. G. GABRIEL.
C. N. HAWKINS.

FRANCIS HEMMING, C.M.G., C.B.E.
J. SMART, B.Sc., Ph.D.

Publication Committee.

O. W. RICHARDS, M.A., D.Sc. (Chairman).

E. A. COCKAYNE, M.A., M.D., F.R.C.P.
G. FOX-WILSON.
A. M. MASSEE, D.Sc.

W. H. T. TAMS.
V. B. WIGGLESWORTH, M.A., B.Ch., M.D.,
F.R.S.

Library Committee.

PROF. P. A. BUXTON, M.A. (Chairman).

E. B. BRITTON.
A. S. CORBET, D.Sc., Ph.D., F.I.C.
B. M. HOBBY, M.A., D.Phil.

F. LAING.
R. W. LLOYD.

Committee for the Protection of British Insects.

W. G. SHELDON (Chairman).

CAPT. E. BAGWELL-PUREFOY.
C. L. COLLENETTE.
W. J. DOW.
J. C. F. FRYER, O.B.E., M.A.

COL. F. A. LABOUCHERE.
N. D. RILEY.
H. M. EDELSTEN (Secretary).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO:

1. **British National Committee for Biology** (Royal Society).
Sir Guy A. K. Marshall, C.M.G., D.Sc., F.R.S., appointed 1939.
Dr. Karl Jordan, F.R.S., appointed 1936.
2. **International Congress of Entomology** (Berlin 1938).
J. C. F. Fryer, O.B.E., M.A. *Francis Hemming, C.M.G., C.B.E.*
A. D. Imms, M.A., Sc.D., F.R.S.
3. **Local Committee of Management of Wicken Fen.**
Mr. H. M. Edelsten. *Mr. E. C. Bedwell.*
[Delegates nominated by Committee for the Protection of British Insects.]
4. **National Trust for Places of Historic Interest or Natural Beauty.**
Mr. W. G. Sheldon, appointed 1922.
5. **New Forest Association.**
Mr. W. Fassnidge, appointed 1934.
6. **Royal Meteorological Society. Phenological Committee.**
Dr. C. B. Williams, appointed 1937.

STUDIES ON THE CHEMISTRY OF PIGMENTS IN THE LEPIDOPTERA, WITH REFERENCE TO THEIR BEARING ON SYSTEMATICS. 1. THE ANTHOXANTHINS

By E. B. FORD, M.A., B.Sc., F.R.E.S.
(Reader in Genetics in the University of Oxford.)

CONTENTS.

	PAGE
1. Introduction to the series	65
2. Introduction to the present paper	67
3. Anthoxanthins in the family PIERIDAE	70
4. Anthoxanthins in the family PAPILIONIDAE	78
5. The occurrence of anthoxanthins in other families	84
6. Summary	88
7. References	89

1. Introduction to the series.

THE chemistry of the pigments occurring in the Lepidoptera has been studied on a number of occasions (for a summary of the literature see Baylis 1924, Verne 1930, Imms 1937, Wigglesworth 1939). It must be admitted, however, that the subject has received far less attention than it deserves in view of its interest. Furthermore, it has rarely been applied to classification and phylogeny. Indeed this seems to have been attempted on three occasions only, by Cockayne (1924) and by Ford (1938a and 1940). Yet with the partial exception of the last, in which a short section was devoted to this topic, these articles were concerned mainly with work devoted to other ends. A survey of the chemistry of pigments in its relation to the classification of the Lepidoptera is much to be desired, and the present series of papers is an attempt to meet this need.

Previous investigators have devoted themselves almost wholly to the chemical analysis of some given pigment in a few species, as in the work of Wieland and others (1933) and of Schöpf and Becker (1933). To this, two notable exceptions must be made. The first of these is the well-known and fundamental work of Hopkins (1895). This was devoted mainly to an investigation of the pterine pigments (p. 67) of the PIERIDAE, which he studied in a number of species. But, in addition, he briefly discussed various types of pigments in several other families, and pointed out that superficially similar effects may be produced in mimic and model by different chemical means. However, the bearing of chemistry on classification was hardly within the scope of his work. Indeed his only reference to this topic seems to be the statement that: "In the apparently strict confinement of these special pigments¹ to the PIERIDAE, we have interesting evidence justifying the customary classification of these insects as a natural group." It may be noticed, however, that the pigments of the PIERIDAE are less closely restricted to that family than Hopkins supposed. It seems highly probable that pterines occur widely elsewhere in the Lepido-

¹ Uric acid, and its soluble murexide-yielding derivatives.

ptera (p. 67); while it will be shown in a later paper that the special red pigment which he noticed in certain PAPILIONIDAE is found in some PIERIDAE. Further, it will be demonstrated in the present account that the peculiar pigment (now recognised as a flavone) which he encountered in the Satyrid *Arge* (= *Melanargia*) *galathea* L. occurs also in the latter family, which he studied so fully and successfully, and is, indeed, characteristic of certain Pierine genera. The second investigation to which special attention must be drawn is that of Cockayne (1924), who made an extensive survey of the distribution in the Lepidoptera of the pigments fluorescent in ultra-violet light. His main object was to provide detailed information on their occurrence throughout the Order: a task which he performed in a remarkably thorough manner. But, in addition, his data enabled him to make a number of useful suggestions on classification and phylogeny.

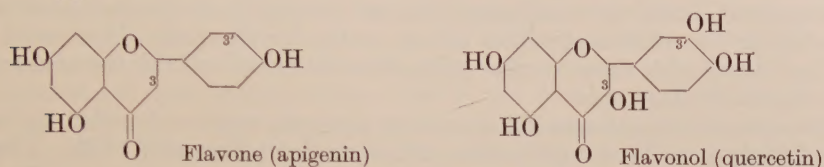
Thus it comes about that to apply chemical methods to the study of systematics in the Lepidoptera is largely to break new ground. I am conscious that the present attempt suffers from the defects inherent in the preliminary treatment of any rather extensive subject. Any detailed investigation of the occurrence of even a single type of pigment in an Order so large as the Lepidoptera would be an immense task, for which I cannot spare the time. Consequently, it has seemed well to proceed upon the following lines. Each pigment has been studied separately, and the work upon it divided into two sections. First, I have examined as thoroughly as possible its distribution within a few convenient families. The data so obtained have then been analysed with respect to the information that they provide both on classification and phylogeny. These detailed studies may be regarded as indicating the kind of results to be obtained from such investigations. Secondly, I have surveyed more widely the occurrence of the pigment in question, but in much less detail: sufficient only to indicate its existence in a number of other groups, for which purpose I have tested a limited selection of species within each. Using such information, those working on one of them may find, for example, that two chemically distinct types of a pigment exist among the insects with which they deal. Seeing that helpful results have been obtained by the application of this fact elsewhere in the Order, they may feel inclined to use it in their own studies.

Several different pigments have already been examined in this way. It is proposed to publish a short series of papers each devoted to one of them, of which this (on the anthoxanthins) is the first. The last is to contain a general summary of the more important results described in the Series. The choice of pigments is restricted by a severe technical limitation. It must be possible to examine them without injuring the specimens studied, otherwise a sufficiently wide range of material could never be obtained. Although confirmatory tests in which this condition is not fulfilled may also be applied, it is one which must be observed in general. Helpful and generous as I have invariably found those in charge of museums to be, it would not be possible for them to facilitate investigations which involve a considerable destruction of the material in their care. It will, however, be realised how severe a handicap on chemical methods such considerations impose.

Naturally it is not suggested that chemistry provides a less fallible criterion of affinity than does structure. The basis of classification should always be as wide as possible, embracing as many characters as are available for study, and to these, chemical distinctions make an addition of some value. In many instances also they corroborate the current classification of the Lepidoptera on evidence wholly distinct from that upon which it has been constructed.

2. Introduction to the present paper.

The anthoxanthins are a group of sap-soluble plant pigments responsible for a series of colours ranging from ivory to deep yellow. Their structure is of the type :



They fall into two classes: the flavones with a hydrogen atom at position 3 in the pyrone ring, and the flavonols in which this is replaced by a hydroxyl. The various types within each group differ from one another by modifications of the side phenyl ring. For example, a hydroxyl substituted at 3' in the flavone illustrated (to give a phenyl ring of the type selected for the flavonol) would convert the ivory apigenin into the yellow luteolin.

These pigments are widespread in plants, but it seems that animals are unable to manufacture them and must obtain them from their food. The ability to digest and use them unaltered is not common, for in general the anthoxanthins are rare in animals. Their existence in the *Lepidoptera* was first recognised by Thomson (1926a) in the Satyrine *Arge galathea* L. He demonstrated also that the same pigment is present in the grass *Dactylis glomerata* upon which the larvae feed (Thomson, 1926b). Since that time Manunta (1935) has shown that anthoxanthins contribute to the cocoon colours of some silkworm races, and that they are found in the blood and epidermis of larvae of the genus *Pieris*. This seems to comprise all the available information on the matter, and it is generally regarded as one on which little is known. Thus Imms (1937: 189) says: "It is probable that pigments of the flavone type are widely spread among insects, but the subject has been very little studied"; while Wigglesworth (1939: 335) remarks: "Anthocyanins² and flavones, which are important flower pigments, are not very common among insects." The results recorded in the present paper, in fact, indicate that anthoxanthins are by no means rare in the *Lepidoptera*. Even here, it appears that the white and yellow colours are usually produced solely by substances very different from them in their origin and chemistry. It is probable that these are "pterines," which are built up from uric acid and, consequently, are manufactured by the insects themselves. They are exemplified by the white "leucopterin" ($C_{19}H_{19}O_{11}N_{15}$) isolated by Wieland and others (1933) from *Pieris brassicae* L., and the yellow "xanthopterin" ($C_{19}H_{19}O_7N_{15}$) obtained by Schöpf and Becker (1933) from the male *Gonepteryx rhamni* L. Hopkins (1895) had regarded the white pigment of the *PIERIDAE* as uric acid, while xanthopterin seems to be the derivative which he named "lepidotic acid." He considered that uric acid and its soluble murexide-producing derivatives are almost restricted to the *PIERIDAE*. Except for *Papilio machaon* L., in which he found that the yellow substance has entirely different properties from the uric acid group, he does not state in what members of other families he investigated the nature of white and yellow pigments. However, white pigments exactly resembling those of the *PIERIDAE* are extremely widespread

² These are sap-soluble glycosides giving a range of colours from scarlet, through purple, to blue. They differ only from the anthoxanthins in the substitution of a hydrogen for an oxygen atom at position 4, to give a γ -pyran instead of a γ -pyrone ring.

in the Lepidoptera. Consequently, one may fully expect to find that many of them are pterines of some type. Their precise nature is irrelevant to the present work, which is concerned to determine whether or not they contain anthoxanthins.

In general, even when anthoxanthins are present they are not alone responsible for the white and yellow colours of the Lepidoptera. It is usual to find that these are due also to other pigments in addition, and this seems always to be true in the PIERIDAE.

The existence of anthoxanthins as wing pigments may be detected by two tests of the type used to recognise them in flowers (Scott-Moncrieff, 1936). First, a yellow colour is produced on fuming the wings with strong ammonia. This is due to the fact that the flavones and flavonols combine with ammonia to form coloured salts. In the Lepidoptera these are very unstable, so that the specimen speedily returns to its original condition after treatment. Consequently, it is uninjured by the process. This reaction is a highly diagnostic and sensitive one. It suffices to detect traces of anthoxanthins when present in a single specimen. In certain circumstances, however, it is inapplicable: when the flavone concerned is itself deep yellow, or when it is obscured by other pigments. In these conditions another method is used. The wings are removed, cut up if necessary, and soaked for at least forty-eight hours in ethyl acetate, which extracts anthoxanthins but not pterines. The colourless solution so obtained is filtered and shaken with an aqueous solution of sodium carbonate, when a deep yellow colour is produced if flavones or flavonols are present. If they are not, the liquid remains colourless. As already explained, a method such as this, which destroys the specimen, cannot be widely used. It is, however, valuable in the circumstances indicated. Moreover, it admits of the accumulation of a detectable amount of pigment from a number of specimens in each of which it exists in a small quantity only. However, it is less sensitive than the former test. The supply of anthoxanthin in the wings of *Enantia licinia* Cr. is considerable, for a deep yellow colour is obtained on fuming them with ammonia. Yet a single specimen does not provide enough pigment to give a positive reaction on extracting with ethyl acetate, though three specimens do contain sufficient to produce a detectable effect. So does even a single specimen of the Satyrine *Arge galathea*.

In general, therefore, I have been able to study only those species possessing colours ranging from white to light yellow. Those in which dark yellow pigment alone is available have been used when it is particularly desirable to establish its nature, provided that sufficient material exists. In all important instances both types of test have been employed where possible. Further, I have made a constant practice of examining several specimens of each species. These have always given consistent results, provided that they are in fairly fresh condition; anthoxanthins are often less easy to demonstrate in worn specimens. On the other hand, the length of time that the insects have been kept in collections appears to be irrelevant. Thus these pigments can be detected as easily in specimens of *Enantia licinia* Cr., preserved at Oxford, which were captured by Burchell in 1827 as in those caught in the present century.

As already indicated, great numbers of species do not use anthoxanthin pigments to form their white or yellow colours. Yet many of them must feed on plants rich in these substances. Either they are unable to digest, or to utilise, them unaltered, or both. The first alternative is inherently possible, for failure to digest a particular type of pigment has been demonstrated

in other circumstances. Thus Gerould (1921) showed that in *Colias philodice* Godt., a single genetic factor, recessive in effect, prevents the digestion of all pigments of the chlorophyll group except the blue-green chlorophyll-A. Similarly, a single factor, also recessive in operation, prevents the Amphipod Crustacean *Gammarus chevreuxi* from digesting carotin, though not from using it when supplied by other means: *i.e.*, in the cytoplasm of the egg (for a full account, see Ford, 1938*b*: 161-65). On the other hand, Manunta (1935) demonstrated that anthoxanthins exist in the blood and epidermis of *Pieris* larvae. Yet the white pigment in the adults of this genus contains none (see p. 72). Furthermore, flavones are present in the white or yellow wings of the genus *Enantia* (p. 76), but in the exposed parts only (though no such restriction occurs in other genera): the areas hidden by the overlap of the fore- and hind-wings are coloured white by pterins in the normal Pierine manner. These two observations tend to show that it is the utilisation rather than the digestion of the flavones and flavonols which determines their presence in the *Lepidoptera*. Such considerations indicate that their occurrence is not dependent merely upon the type of larval food: a fact sufficiently attested by their presence or absence throughout large groups with varied food-plants (e.g., *Graphium* compared with *Papilio*). Furthermore, numerous instances exist of two species one of which possesses anthoxanthin pigment in the scales while the other does not, though they have the same food-plant (e.g., *Pararge egeria* L. and *Coenonympha pamphilus* L. Anthoxanthins are absent in the former but present in the latter. They both feed in grasses, especially *Poa annua*, on which each has been reared).

I have made rather thorough studies of the occurrence of anthoxanthins in the PAPILIONIDAE and the PIERIDAE, and have used the data so obtained to throw light on the systematics of these two families. I have also surveyed a number of other groups of *Lepidoptera*, but in sufficient detail only to indicate the presence of anthoxanthins in them, according to the plan already described. The work has been conducted on the material in the Hope Department of Entomology at Oxford, and in the Department of Entomology at the British Museum (Natural History). I have also had the benefit of examining additional species in the Rothschild Museum at Tring (now a branch of the British Museum). These three collections together contain so overwhelming a proportion of the *Lepidoptera* of the world preserved in Great Britain that to examine others after them would be unnecessary.

Acknowledgments.

I should like to express my most grateful thanks to Prof. G. D. Hale Carpenter for placing at my disposal the resources of the Hope Department of Entomology at Oxford, where these investigations have principally been conducted, and for the help and encouragement which he has always been so ready to give. I am also deeply indebted to Mr. N. D. Riley, Keeper of Entomology at the British Museum (Natural History), for allowing me to make full use of the National Collection of *Lepidoptera*. Without the co-operation of those in charge of the great museums, such work as this could never be undertaken.

It is a pleasure to record the valuable help which I have received from a number of experts. I especially wish to mention Mr. G. Talbot, whose exceptional knowledge, particularly of the PAPILIONIDAE and the PIERIDAE, has been of great assistance to me, Mr. A. G. Gabriel, who has given me his help on many occasions, and Dr. A. S. Corbet, whose views I have been so glad to obtain.

They have all been so good as to give me the benefit of their opinion on this paper. I have had the advantage of discussing the bearing of chemistry on classification in the PAPILIONIDAE with Dr. K. Jordan, F.R.S. Mr. W. H. T. Tams has been so kind as to give me his help in the section which deals with the moths.

I am much indebted to Dr. B. K. Blount for his kind help on chemical questions. I have had the pleasure of discussing this paper with Prof. R. A. Fisher, F.R.S. His suggestions, and the interest which he has taken in the work, have been a great encouragement to me. I should like to thank Prof. E. S. Goodrich, F.R.S., for his helpful criticism.

3. Anthoxanthins in the family PIERIDAE.

The PIERIDAE comprise the great assemblage of the white and sulphur butterflies and their allies. I have followed, in my study of them, the most modern classification dealing with the family throughout its entire range: that of Talbot (1932-35) in *Lepidopterorum Catalogus*. In a still more recent work, the same author (Talbot, 1939) has made certain minor adjustments to his previous scheme. However, as he was there treating of the butterflies of British India alone, it has seemed well to follow the former work throughout. It would be in several ways unsatisfactory to modify a small section only of the arrangement; and there is some advantage in basing the present discussion on a single well-known and authoritative plan.

In *Lepidopterorum Catalogus* the family is divided into five subfamilies, in the following order:—

- | | |
|-----------------------------|------------|
| 1. PSEUDOPONTIINAE E. Reut. | (1 genus) |
| 2. DISMORPHIINAE Hübn. | (3 genera) |
| 3. PIERINAE Sw. | (43 „) |
| 4. TERACOLINAE Auriv. | (9 „) |
| 5. COLIADINAE Auriv. | (11 „) |

The first of these contains but a single genus and species, the unique African *Pseudopontia paradoxa* Feld. I have not detected anthoxanthins in this form, and indeed its scales are greatly reduced. The second comprises the peculiar central and South American genera *Dismorphia* (now to be sub-divided, p. 74) and *Pseudopieris* and, in addition, the Palaearctic “Wood Whites” (*Leptidea*): 108 species in all. They are highly abnormal Pierids. The remaining three subfamilies must include many hundreds of species.

It may be added that Talbot (1939) no longer distinguishes the TERACOLINAE as a separate subfamily but combines them with the COLIADINAE. However, as will later appear (p. 77), there seems to be some advantage in separating the PIERINAE and TERACOLINAE, principally feeding on Cruciferae and Capparidaceae respectively, from the COLIADINAE (in the strict sense) which feed on Leguminosae. In addition, to do so is in accord with the classification which has been adopted here.

I have elsewhere reported the discovery of anthoxanthin pigments in some species of the subfamily DISMORPHIINAE, and their apparent absence elsewhere in the PIERIDAE, and have commented on the significance of this fact (Ford, 1940). A great deal more information on the subject is now available.

First, it may be well to consider the negative evidence derived from the remainder of the PIERIDAE. Time would not have allowed me to examine every suitable species available in the subfamilies PIERINAE, TERACOLINAE, and

TABLE 1.

Genera and species tested for anthoxanthins in the subfamily PIERINÆ.

Genus	Species	Genus	Species
<i>Neophasia</i>	<i>menapia</i> Feld.	<i>Appias</i>	<i>lyncida</i> Cr.
<i>Catasticta</i>	<i>corcyra</i> Feld.		<i>celestina</i> Bdv.
	<i>ctemene</i> Hew.		<i>cardena</i> Hew.
	<i>sisamnus</i> Fb.		<i>paulina</i> Cr.
	<i>flisa</i> H.-S.		<i>leis</i> Hbn.
	<i>philone</i> Feld.		<i>epaphia</i> Cr.
	<i>teutila</i> Dbl.	<i>Phrissura</i>	<i>aegis</i> Feld.
	<i>tomyris</i> Feld.	<i>Saletara</i>	<i>panda</i> Godt.
	<i>toca</i> Dbl.	<i>Andropodum</i>	<i>drusilla</i> Cr.
<i>Leodonta</i>	<i>dysoni</i> Dbl.	<i>Anapheis</i>	<i>creona</i> Cr.
<i>Archonias</i>	<i>tereas</i> Godt.		<i>grandidieri</i> Mab.
<i>Charonias</i>	<i>theano</i> Bdv.		<i>antsianaka</i> Ward
<i>Pereute</i>	<i>charops</i> Bdv.	<i>Belenois</i>	<i>raffrayi</i> Ob.
<i>Leptophobia</i>	<i>erinna</i> Hopf		<i>margaritacea</i> Shpe.
	<i>pentthica</i> Koll.		<i>calypso</i> Drury
<i>Melete</i>	<i>lycimnia</i> Cr.	<i>Dixeia</i>	<i>orbona</i> Geyer
	<i>leucanthe</i> Feld.		<i>pigea</i> Bdv.
<i>Tatochila</i>	<i>autodice</i> Hb.		<i>charina</i> Bdv.
<i>Phulia</i>	<i>nymphula</i> Blanch.	<i>Ascia</i>	<i>monuste</i> L.
<i>Piercolias</i>	<i>huanaco</i> Stgr.		<i>sevata</i> Feld.
<i>Baltia</i>	<i>shawi</i> Bates		<i>buniae</i> Hbn.
<i>Mesapia</i>	<i>peloria</i> Hew.		<i>amaryllis</i> Fb.
<i>Aporia</i>	<i>crataegi</i> L.	<i>Itaballia</i>	<i>demophile</i> L.
	<i>soracta</i> Moore		<i>pandosa</i> Hew.
	<i>delavayi</i> Ob.	<i>Perrhybris</i>	<i>pyrrha</i> Cr.
	<i>largeteau</i> Ob.		<i>lorena</i> Hew.
<i>Delias</i>	<i>georgina</i> Feld.	<i>Pieris</i>	<i>brassicae</i> L.
	<i>castaneus</i> Kenr.		<i>candida</i> Sparrm.
	<i>bornemanni</i> Ribbe		<i>rapae</i> L.
	<i>bakeri</i> Kenr.		<i>extensa</i> Pouj.
	<i>callima</i> R. & J.		<i>melete</i> Men.
	<i>kummeri</i> Ribbe		<i>napi</i> L.
	<i>oryntion</i> G. & S.		<i>mandela</i> Feld.
	<i>nigrina</i> Fb.	<i>Mylothris</i>	<i>chloris</i> Fb.
	<i>henningsia</i> Esch.		<i>rembina</i> Ploetz
	<i>crithoe</i> Bdv.		<i>poppea</i> Karsch.
	<i>aglaia</i> L.		<i>agathina</i> Cr.
	<i>egialea</i> Cr.		<i>rueppellii</i> G. Koch
	<i>thysbe</i> Cr.		<i>phileris</i> Bdv.
	<i>descombesi</i> Bdv.		<i>trimenia</i> Btl.
	<i>belisama</i> Cr.		<i>sagala</i> Sm.
	<i>eumolpe</i> Sm.	<i>Nina</i>	<i>nina</i> Fab.
	<i>aruna</i> Bdv.	<i>Elodina</i>	<i>hypatia</i> Feld.
	<i>aganippe</i> Don.		<i>parthia</i> Hew.
	<i>harpalyce</i> Don.	<i>Leuciactria</i>	<i>acuta</i> R. & J.
	<i>agostina</i> Hew.	<i>Synchlœ</i>	<i>callidice</i> Esp.
	<i>ennia</i> Wall.	<i>Pontia</i>	<i>daphidice</i> L.
s.g. <i>Cathaemia</i>	<i>eucharis</i> Drury		<i>helice</i> L.
	<i>hyparete</i> L.	<i>Pontieuchloia</i>	<i>chloridice</i> Hb.
	<i>mysis</i> L.	<i>Zegris</i>	<i>eupheme</i> Esp.
	<i>argenthona</i> Fb.	<i>Euchloe</i>	<i>ausonia</i> Hbn.
<i>Cepora</i>	<i>nerissa</i> Fb.		<i>belemia</i> Esp.
	<i>nadina</i> H. Luc.		<i>creusa</i> Dbl.
	<i>perimale</i> Don.	<i>Elphinstonia</i>	<i>tagis</i> Hbn.
	<i>boisduvaliana</i> Feld.	<i>Anthocharis</i>	<i>cardamines</i> L.
<i>Aoa</i>	<i>affinis</i> Voll.		<i>belia</i> L.
<i>Udaiana</i>	<i>cynis</i> Hew.		<i>sara</i> Bdv.
<i>Ixias</i>	<i>pyrene</i> L.	s.g. <i>Falcapica</i>	<i>genutia</i> Fab.
<i>Prioneris</i>	<i>sita</i> Feld.		<i>scolymus</i> Btl.
	<i>autothisbe</i> Hb.	<i>Pinacopteryx</i>	<i>eriphia</i> Godt.
	<i>hypsipyle</i> Weym.		
<i>Appias</i>	<i>libythea</i> Fb.	43 genera	122 species

TABLE 2.

Genera and species tested for anthoxanthins in the subfamily TERACOLINAE.

Genus	Species	Genus	Species
<i>Eroessa</i>	<i>chilensis</i> Guér.	<i>Colotis</i>	<i>daira</i> Klug
<i>Hesperocharis</i>	<i>nera</i> Hew.		<i>etrida</i> Bdv.
	<i>anguitia</i> Godt.		<i>evenina</i> Wllgr.
	<i>erota</i> Luc.		<i>eris</i> Klug
	<i>marshalii</i> Guér.		<i>subfasciatus</i> Sws.
s.g. <i>Cunizza</i>	<i>hirlanda</i> Stoll	s.g. <i>Calopieris</i>	<i>eulimene</i> Klug
s.g. <i>Mathania</i>	<i>leucothea</i> Molina	<i>Gideona</i>	<i>lucasi</i> Grand.
<i>Eucheira</i>	<i>socialis</i> Westw.	<i>Eronia</i>	<i>cleodora</i> Hbn.
<i>Colotis</i>	<i>phisadia</i> Godt.		<i>leda</i> Bdv.
	<i>vestalis</i> Btl.	<i>Nepheronia</i>	<i>argia</i> Fb.
	<i>vesta</i> Riche		<i>buqueti</i> Bdv.
	<i>celimene</i> Luc.		<i>pharis</i> Bdv.
	<i>halimede</i> Klug		<i>thalassina</i> Bdv.
	<i>pleione</i> Klug		<i>avatar</i> Moore
	<i>ione</i> Godt.		<i>hippia</i> Fab.
	<i>ketaera</i> Gerst.	<i>Pareronia</i>	<i>glaucippe</i> L.
	<i>danae</i> Fb.	<i>Hebomoia</i>	
	<i>eucharis</i> Fb.		
	<i>evippe</i> L.		
		9 genera	35 species

COLIADINAE. I have therefore taken samples from every one of the sixty-three genera into which they are divided by Talbot (1932-35). In all but the smallest of these I have studied numerous species, making sure that those selected are widely scattered through the genus, and that they are drawn from each subgenus suitable for study where such exist. The genera and species (amounting to 63 and 195 respectively) so examined are given in Tables 1-3. I may perhaps claim that this represents a fairly thorough survey of the three subfamilies in question.

In no instances save two have anthoxanthin pigments been detected in them. These exceptions are first, *Gandaca* (COLIADINAE), a genus of a single species (*G. harina* Horsf.) containing abundant pigment of the flavone type.³ The problems which it presents will be reserved for discussion later (p. 77). Secondly, the African *Eronia cleodora* Hbn. (TERACOLINAE), in which, however, the situation is very different, since the quantity of anthoxanthin pigment which it contains is quite minute. It might easily escape notice, as a barely detectable trace only can be demonstrated, by the ammonia method, in none but very fresh specimens. The situation, therefore, is quite unlike that found in the other PIERIDAE which possess these pigments, for in them they are easily recognised. I was able to obtain 18 specimens of *E. cleodora* for extraction with ethyl acetate, but the quantity of pigment is too small to be detected by this means. Consequently it cannot be as much as one-sixth of that present in *Enantia licinia* (see p. 76), a smaller butterfly, and may be much less than this. Interest naturally attaches to the only other species of the genus *Eronia*. This is *E. leda* Bdv. Unfortunately the males are bright yellow insects with orange tips to the fore-wings, so that the ammonia test is inapplicable to them. The females are paler, but they give no reaction by this method: they are, however, too deeply coloured for a slight effect to be detected. Eighteen

³ On extraction with ethyl acetate, 3 specimens produce a detectable effect, so that the quantity of anthoxanthin is nearly the same as in the *Enantia* species (p. 76).

TABLE 3.

Genera and species tested for anthoxanthins in the subfamily COLLADINAE.

Genus	Species	Genus	Species
<i>Colias</i>	<i>palaeno</i> L. <i>philodice</i> Godt. <i>hyale</i> L. <i>electo</i> L. <i>e. croceus</i> Fourc. <i>dimera</i> D. & H. <i>vautieri</i> Guer.	<i>Gandaca</i>	<i>harina</i> Horsf.
<i>Catopsilia</i>	<i>pomona</i> Fb. <i>sylla</i> L. <i>gorgophone</i> Bdv. <i>pyranthe</i> L. <i>florella</i> Fb.	<i>Eurema</i>	<i>hecabe</i> L. <i>candida</i> Cr. <i>daira</i> Godt. <i>agave</i> Cr. <i>elathea</i> Cr. <i>phiale</i> Cr. <i>arbela</i> Gey. <i>gratiosa</i> D. & H. <i>mexicana</i> Bdv. <i>adamsi</i> Lathy <i>albula</i> Cr. <i>deva</i> Dbl. <i>priddyi</i> Lathy <i>hisa</i> B. & L. <i>nise</i> Cr. <i>messalina</i> Fab. <i>iole</i> Bdv.
<i>Anteos</i>	<i>clorinde</i> Godt.		
<i>Gonepteryx</i>	<i>rhamni</i> L. <i>cleopatra</i> L.		
<i>Dercas</i>	<i>lycorias</i> Dbl.		
<i>Phoebis</i>	<i>sennae</i> L. <i>argante</i> Fab. <i>castalis</i> Fab.	<i>Nathalis</i>	
<i>Kricogonia</i>	<i>brephos</i> Hbn.		
<i>Leucidia</i>		11 genera	38 species

specimens were available for pigment extraction, but the result was negative. Therefore it is only possible to assert that the wings of *E. leda* cannot contain more than a trace of pigment of the flavone type, and may contain none. *Gandaca harina* and *Eronia cleodora* are the only species among the PIERIDAE in which I have found anthoxanthins outside the genera of which such pigments are characteristic: 2 out of 233 species.

Attention may now be devoted to the remaining subfamily, the DISMORPHIINAE. Talbot (1932-35) includes 102 species in the genus *Dismorphia*, some of which I find contain anthoxanthins. So too do all three species (see Table 4) of the closely allied, and also neotropical, genus *Pseudopieris*. These two genera are exceedingly distinct from the remaining PIERIDAE and many, but not all, of the species are mimetic. The question of their relation to the rest of the group is therefore one of considerable interest. Structural considerations have led to the rather remarkable conclusion that they are allied to the Palaearctic "Wood Whites" *Leptidea*. Thus Röber (1924: 98) says: "With this genus [*Pseudopieris*] begins a small group of genera which cannot with certainty be reckoned Pierids and yet can still less be associated with any other family. . . . Their nearest representatives are the Palaearctic *Leptidea* and perhaps *Pseudopontia* from West Africa." Talbot (*loc. cit.*) goes further, and includes *Leptidea* in the subfamily DISMORPHIINAE. Doubtless he is right, for the genus contains abundant anthoxanthins, a condition never found elsewhere in the PIERIDAE (save in *Gandaca*, p. 72) outside the neotropical DISMORPHIINAE. On extraction with ethyl acetate, three specimens of *Leptidea sinapis* provide a sufficient quantity of anthoxanthin to produce a just detectable effect. The amount present is therefore approximately the same as in *Enantia* (pp. 74-76) and *Pseudopieris* (for I obtained a similar result on extracting anthoxanthins from 3 specimens of *P. nehamia*). Antho-

xanthins are easily detected in all three species of *Leptidea*⁴ (see Table 4), indicating that its occurrence is fundamental to the genus and not to be treated as a stray exception. It will be noticed that chemical considerations here support in a striking manner an affinity suggested on purely structural grounds.

Having established these facts, the distribution of anthoxanthins within the genus *Dismorphia* became a matter of importance. Would the species containing them be scattered at random on the present classification, or would they fall into a more or less compact group? The latter alternative has proved correct. It indicates a close correlation between the classificatory value of structural and physiological characters in these insects. I have examined every species of *Dismorphia* suitable for study to which I have had access, amounting to 50 out of 102. Of these, twelve contain anthoxanthins and, save for the interpolation of *thermesia* Godt. (see below), they all fall together at the beginning of the genus. Not a single species possesses these pigments among the 37 tested which follow them (see Table 4).

It is a remarkable fact that in a family such as the PIERIDAE, in which pterins are normally responsible for the white and yellow colours, there should exist a group of species which possess pigments differing from them so profoundly in chemistry and origin as the anthoxanthins. When it is further considered that this distinction is intimately related to the accepted classification, though this was devised in ignorance of it, it may be seen that the difference involved is an important one and far greater than any usually to be found between related genera. It is plain therefore that the group of *Dismorphia* species which contain anthoxanthins should be separated generically from the remainder. As pointed out to me by Mr. A. G. Gabriel, a generic name suitable for them already exists. This is *Enantia* (Hüb., 1819, *Verz. bek. Schmett.* : 96) with *licinia* Cr. as type species. *Dismorphia* (Hüb., 1816, *ibid.* : 10), with *laia* Cr. as type, is applicable to the remaining, and much larger, section of the present genus. It is not in their chemistry alone that *Enantia* and *Dismorphia* can be distinguished. The former genus contains species whose ground-colour is always pale, ranging from ivory to deep yellow, sometimes flushed with orange. Also they are marked with black in a fairly regular manner. The latter comprises very varied forms, many being mimetic, but none having quite the *Enantia* colour-pattern.

Reference to Table 4 will show that among the species at present placed in *Enantia* is one, *thermesia* Godt., which must have been classified incorrectly. It is clearly to be distinguished from them because it contains no anthoxanthins. It was on this chemical evidence that the error was detected, but further inspection reveals other differences. On the upperside, the male bears a dark transverse bar across the disc of the fore-wings, and a brown oblong scent-patch near the costa of the hind-wings. Neither of these characters occurs in *Enantia*, but they are found in several *Dismorphia* species. If *thermesia* be placed in the latter genus between *pallidula* Btl. and *lysis* Hew., it will be found to accord very well with its new position. In the male, both these insects possess the brown scent-patch on the hind-wings, and the transverse band is seen as a dark mark on the brownish-black fore-wings of *pallidula* while it invades the white discal region of *lysis*. All three are black (or brownish) and white species; furthermore, the shape of *thermesia* and *lysis* is very similar in both sexes.

⁴ Röber (1907-8) regards *L. amurensis* Men. as specifically distinct, making a fourth *Leptidea*. However, Talbot (*loc. cit.*) treats it as a subspecies of *L. sinapis* L. For my purpose the point is immaterial, since *L. amurensis* contains anthoxanthins as do the rest of the genus.

TABLE 4.

The genera and species of the subfamily DISMORPHIINAE arranged according to Talbot (1932-35). + = anthoxanthins present, — = anthoxanthins absent. Unmarked species have not been tested.

1. <i>Dismorphia</i> Hbn.					
1. <i>flavia</i> Feld.	+		58. <i>spio</i> Godt.		
2. <i>psamathe</i> Fb.	+		59. <i>cubana</i> H.-Sch.		
3. <i>acutipennis</i> Btl.	+		60. <i>lysianax</i> Hew.		
4. <i>mercenaria</i> Feld.	+		61. <i>tricolor</i> Sm. & Kby.		
5. <i>licinia</i> Cr.	+		62. <i>spectabilis</i> Avin.		
6. <i>lina</i> Herbst			63. <i>mechanitina</i> Rüb.		
7. <i>aphrodite</i> Feld.	+		64. <i>xanthone</i> Rüb.		
8. <i>marion</i> G. & S.	+		65. <i>amphione</i> Cr.		—
9. <i>thermesia</i> Godt.	—		66. <i>laia</i> Cr.		
10. <i>limnorina</i> Feld.	+		67. <i>astynome</i> Dalm.		—
11. <i>dilis</i> Bdv.			68. <i>astyocha</i> Hb.		
12. <i>dissimulata</i> d'Almeida			69. <i>deione</i> Hew.		—
13. <i>theugenis</i> Dbl.	+		70. <i>eunoe</i> Dbl.		
14. <i>melite</i> L.	+		71. <i>sororna</i> Btl.		
15. <i>cornelia</i> Feld.	+		72. <i>myris</i> G. & S.		
16. <i>albania</i> Bates	+		73. <i>cordillera</i> Feld.		
17. <i>mirandola</i> Hew.	—		74. <i>orise</i> Bdv.		—
18. <i>altis</i> Fassl			75. <i>rhetes</i> Hew.		
19. <i>carthesis</i> Hew.			76. <i>clio</i> Cr.		
20. <i>idonia</i> Hew.			77. <i>siloe</i> Hew.		
21. <i>zaela</i> Hew.			78. <i>theucharila</i> Dbl.		
22. <i>arcadia</i> Feld.	—		79. <i>lysinoë</i> Hew.		
23. <i>lucilla</i> Btl.			80. <i>lysinoides</i> Stgr.		
24. <i>crisia</i> Drury	—		81. <i>erythoe</i> Bates		
25. <i>core</i> Feld.	—		82. <i>pellucida</i> Rüb.		
26. <i>medora</i> Dbl.	—		83. <i>batesi</i> Rüb.		
27. <i>albimacula</i> Rüb.			84. <i>leuconoe</i> Bates		—
28. <i>ideae</i> Fassl			85. <i>fortunata</i> H. Luc.		—
29. <i>proserpina</i> Sm. & Kby.			86. <i>ribbei</i> G. & S.		
30. <i>zathoe</i> Hew.			87. <i>alterata</i> Btl.		
31. <i>lelex</i> Hew.	—		88. <i>antherize</i> Hew.		—
32. <i>pimpla</i> Hopff.	—		89. <i>avonia</i> Hew.		—
33. <i>pallidula</i> Btl.	—		90. <i>wernerii</i> Hering		
34. <i>lysis</i> Hew.	—		91. <i>limonea</i> Btl.		
35. <i>foedora</i> H. Luc.	—		92. <i>leuconia</i> Btl.		
36. <i>virgo</i> Bates	—		93. <i>pinthaeus</i> L.		—
37. <i>lua</i> Hew.	—		94. <i>ithomia</i> Hew.		—
38. <i>garleppi</i> Stgr.	—		95. <i>theaphina</i> Btl.		
39. <i>lycosura</i> Hew.	—		96. <i>methymna</i> Godt.		
40. <i>schausii</i> Dogn.	—		97. <i>cyra</i> Dbl.		
41. <i>leonora</i> Hew.	—		98. <i>naphra</i> Herr.-S.		
42. <i>macasana</i> Strand			99. <i>elongatus</i> Goeze		
43. <i>niepelti</i> Wegm.	—		100. <i>nemesis</i> Latr.		—
44. <i>lewyi</i> Luc.	—		101. <i>cinerascens</i> Salv.		—
45. <i>dolorita</i> Fassl	—		102. <i>poasina</i> Schs.		
46. <i>critomedia</i> Geyer	—				
47. <i>euryope</i> H. Luc.	—		2. <i>Pseudopieris</i> G. & S.		
48. <i>ines</i> Rüb.	—		1. <i>nehemia</i> Bdv.		+
49. <i>oreas</i> Salv.			2. <i>penia</i> Hopff.		+
50. <i>lygdamis</i> Hew.	—		3. <i>limbalis</i> Rüb.		+
51. <i>hyposticta</i> Feld.					
52. <i>manuelita</i> Fassl			3. <i>Leptidea</i> Billb.		
53. <i>hippotas</i> Hew.	—		1. <i>sinapis</i> L.		+
54. <i>abilene</i> Hew.	—		(<i>amurensis</i> Men.)		+
55. <i>teresa</i> Hew.	—		2. <i>duponcheli</i> Stgr.		+
56. <i>melia</i> Godt.	—		3. <i>gigantea</i> Leech		+
57. <i>larunda</i> Hew.					

With the above adjustment, and following the order of species in the sub-family DISMORPHIINAE as adopted in *Lepidopterorum Catalogus*, one obtains four genera, *Enantia*, *Dismorphia*, *Pseudopieris*, and *Leptidea*, three of which without exception contain flavones, while one, the second, without exception, does not. Clearly this arrangement is unnatural. However, if *Leptidea* be placed first and *Pseudopieris* second, all irregularities are removed. There are then three consecutive genera possessing flavones, preceding one which, like the normal Pierine genera that follow it, is without them. Also by placing the Palaearctic *Leptidea* first, the neotropical genera can be kept together.

I shall now consider the genus *Enantia* in detail. Since the publication of the sections on the PIERIDAE in *Lepidopterorum Catalogus*, Talbot has come to the conclusion that some of the forms there separated as species are of subspecific rank only. This arrangement is now adopted at the British Museum, and should be substituted for that previously published. It in no way affects the conclusions reached in this paper. The new system is given in Table 5.

TABLE 5.

The genus *Enantia* Hbn.

Species	Subspecies
<i>licinia</i> Cr.	<i>psamathe</i> Fabr. <i>mercenaria</i> Feld. <i>licinia</i> Cr. <i>lina</i> Herbst <i>aphrodite</i> Feld. <i>dilis</i> Bdv. <i>marion</i> G. & S. <i>acutipennis</i> Btl.
<i>limnorina</i> Feld.	—
<i>dissimulata</i> d'Almeida	—
<i>theugenis</i> Dbl.	—
<i>melite</i> L.	<i>flavia</i> Feld. <i>melite</i> L. <i>cornelia</i> Feld. <i>albania</i> Bates

It will be seen that *licinia* now includes eight forms treated as sub-specifically distinct by Talbot (1932-35). The ground-colour is a pale yellowish-cream in all. The species gives a striking flavone reaction with ammonia. On extracting with ethyl acetate, 3 specimens supply a sufficient quantity of the pigment to produce a just detectable effect. I have placed *acutipennis* next to *marion*, from which it is separated in *Lepidopterorum Catalogus*, as these two subspecies are evidently closely allied, and Mr. G. Talbot informs me that he is in agreement with this alteration.

E. limnorina is a very distinct species. Its pale ground-colour allows the immediate demonstration of its anthoxanthins by means of the ammonia test.

E. dissimulata is unknown to me.

E. theugenis is a somewhat uncommon species. The ground-colour is usually deep yellow, but a single specimen in the British Museum was pale enough for the demonstration of its anthoxanthins by means of the ammonia test. However, their presence can always be proved by extraction with ethyl acetate, 3 specimens being sufficient for this purpose.

E. melite has a ground-colour ranging from deep yellow, sometimes suffused with orange, to ivory. Anthoxanthins are easily demonstrated by ammonia in the whitish form *alba* Rüb., and in the palest of subspecies *albana*. They can also be detected in the deep yellow forms by extraction with ethyl acetate. Three specimens produce a definite effect, so that the total quantity appears to be approximately the same as in the other species of the genus.

Röber (1909) mentions, and figures, *citrinella* Feld. which he described as "a species scarcely differing from *melite*." Its ground-colour is of a sulphur shade. Talbot (1932-35) regards the name as a synonym either of *flavia* Feld. or of *albana* Bates. The latter comprises forms of *melite* generally paler than the description of *citrinella* indicates; while the former agrees very well with the description of *citrinella*. However, *flavia* (Feld., 1861, *Wien. ent. Monats.* 5 : 76) has page priority over *citrinella* (*ibid.* : 77) and should be used for this form. There is no reason to think it specifically distinct from *melite*.

As already pointed out (p. 72), *Eronia cleodora* and *Gandaca harina* are the only Pierid species possessing anthoxanthins as wing pigments outside the genera *Leptidea*, *Pseudopieris*, and *Enantia*, in which they are invariably found. It may reasonably be supposed therefore that they merely represent very rare exceptions. It is just possible, however, that the latter species may be in rather a different position from the former in this respect. *Eronia* is quite closely allied to the neighbouring genera, while the amount of anthoxanthin present in the wings of *E. cleodora* is minute, unlike the genera of which this type of pigment is characteristic. However, *Gandaca* is an isolated genus, as indicated by its venation (Talbot, 1939). It was formerly included in the genus *Eurema*, some species of which it closely resembles. But this similarity is purely superficial. Brigadier W. H. Evans informs me that he has long realised that it is entirely distinct from them : a conclusion first suggested by its very different habits. This is now supported by the chemical evidence presented by the present work.

It is just possible therefore that the possession by *Gandaca harina* of abundant anthoxanthins indicates some affinity with the DISMORPHIINAE. If so, its nearest ally among the latter subfamily is presumably *Leptidea*, the only Asiatic (Palearctic) genus of DISMORPHIINAE, for *G. harina* inhabits the Oriental Region (ranging from north-eastern India and Burma to New Guinea). Its food-plant is not known, but it is probably one of the Leguminosae, as is characteristic of the COLIADINAE to which it belongs. I can find no information on the food-plants of the neotropical DISMORPHIINAE; but *Leptidea* also feeds on Leguminosae, whereas the TERACOLINAE and PIERINAE are predominantly feeders on Capparidaceae and Cruciferae respectively.

It might be possible, therefore, to regard *Gandaca* as the most primitive of the COLIADINAE and to remove this genus to the end of the subfamily, allying it distantly with the genus *Leptidea* in the DISMORPHIINAE. Mr. G. Talbot informs me that he sees no objection to such an alteration. This would place the DISMORPHIINAE closer to the COLIADINAE than to any other group. One might consequently arrange the subfamilies of the PIERIDAE in the following sequence : 1 PIERINAE, 2 TERACOLINAE, 3 COLIADINAE (ending with *Gandaca*), 4 DISMORPHIINAE (beginning with *Leptidea*, see p. 73), 5 PSEUDOPONTIINAE whose position is arbitrary. The TERACOLINAE are very close to the COLIADINAE, indeed Talbot (1939) considers that they are not even separable from them. However, it may be a convenience to retain them as distinct, since they differ from the COLIADINAE (as from the PIERINAE) in their food-plants, which principally belong to the Capparidaceae. Though I should not at all wish to

stress the suggestion that *Gandaca* is other than an exception in its possession of abundant anthoxanthins, the possibility just considered should at least be borne in mind in considering the interrelationships of the family.

The application of chemical methods to the classification of the PIERIDAE has been of use in several ways. It has confirmed the relationship of the Palaearctic "Wood Whites" (*Leptidea*) with the Central and South American DISMORPHIINAE. It has provided a natural order for the genera of this subfamily, previously arranged almost at random. It has distinguished, upon rather clear evidence, two genera (*Enantia* and *Dismorphia*) which had been wrongly combined. It has corrected an error in the classification of a species (*Dismorphia thermesia*); and it has confirmed the opinion that *Gandaca* is an isolated genus not closely allied to *Eurema*. Furthermore, it has suggested at least possible affinities between subfamilies hitherto quite arbitrarily grouped. These results might not have been attained by other means.

4. Anthoxanthins in the family PAPILIONIDAE.

The bearing of chemistry on classification in the PAPILIONIDAE cannot be studied without a detailed consideration of two important types of red pigment (Ford, 1940). Consequently, little but the data on the occurrence of anthoxanthins in the family will be presented now. Except for a few points which can be discussed at once, its significance will be reserved for treatment in the next paper of this series, which is to deal with the red pigments in question. Thus it has seemed well to place the PIERIDAE first in this article as a family in which the work on anthoxanthins could be carried to completion, and to deal with the mere distribution of these pigments in the PAPILIONIDAE afterwards.

The classification of the PAPILIONIDAE adopted here is that used in the appropriate sections of the *Macrolepidoptera of the World* (Seitz, 1907; Jordan, 1907, 1908-9; Aurivillius, 1908, 1910). The species are therefore grouped according to faunistic regions. The following minor alterations are, however, made: (1) The three sections into which the genus *Papilio* is divided in that work are treated as separate genera here, following Talbot (1939). (2) Prior names are substituted for two of these, and for other genera where necessary. (3) The "Aristolochia Swallowtails" (the "Pharmacophagus Section" of the *Macrolepidoptera of the World*) are divided into two genera *Troides* and *Polydorus* (see Talbot, *loc. cit.*) No changes other than these have been made in the arrangement of the *Macrolepidoptera of the World*.

Talbot (1939) divides the "Fluted Swallowtails" into two genera: *Chilasa* and *Papilio*. This procedure, which is not adopted here, will be discussed in the next paper of this series, in which it is hoped to review the classification of the PAPILIONIDAE in detail.

The most recent revision of the PAPILIONIDAE is that of Talbot (1939), but it is restricted to British India. Two classifications of the family covering its entire range have appeared during the present century, those of the *Macrolepidoptera of the World* itself, and of Bryk (1923-30). However, the latter does not even distinguish the "Kite Swallowtails" (*Graphium*), nor does it divide the species into the numerous groups adopted by Jordan (1907, 1908-9) and Aurivillius (1908, 1910). Not only are these convenient, but there is good evidence to show that some at least of them form natural assemblages. Consequently, with the adjustments already noted, the arrangement of the *Macrolepidoptera of the World* will be followed strictly for the present.

The four genera into which the single genus *Papilio* of the latter work is now divided are: 1. *Troides* Hb., 1819 (= *Ornithoptera* Bdv., 1832); 2. *Polydorus*

Swainson, 1833. (These two genera comprise the "Aristolochia Swallowtails," i.e., *Pharmacophagus* Haase, 1892.) 3. *Papilio* L., the "Fluted Swallowtails"; 4. *Graphium* Scopoli 1777 (= *Cosmodesmus* Haase, 1892), the "Kite Swallowtails."

The first two of these genera are, of course, much the most closely allied. The above order is that in which the corresponding groups are placed by Jordan (1907, 1908-9), but Aurivillius (1908, 1910) interchanges the *Aristolochia* and the Fluted Swallowtails. It will be shown in the next paper of this series that the latter arrangement is probably to be preferred.

I have examined 116 species of *Papilio* (s.s.), drawn from the entire range of the genus, without finding anthoxanthins in any of them. Since this large sample contains no exceptions, the list of those tested is omitted, in order to save excessive tabulation. Similarly, it appears unnecessary to list the species of *Troides* examined, since these comprise the majority of the genus (19 out of approximately 27) and none possessing anthoxanthins was found. However, *Polydorus* and *Graphium* both contain exceptions which make it essential that the data upon these genera should be supplied in full. They are given in Tables 6-8. A summary of the results is provided in Table 9.

It will be seen that *Papilio* and *Troides* are invariably without anthoxanthins. These pigments are generally absent from *Polydorus* also. However, when present, their occurrence in the latter genus is not uniform, for they are restricted to the New World species, among which they are predominantly found in the Aeneas group. The relation between the distribution of these pigments and accepted classification is further indicated by the fact that the only species, two in number, in which I have found anthoxanthins outside the Aeneas group belong to groups placed on either side of it.

When anthoxanthins occur in *Polydorus* species, they do so in a very different way from that of all other genera of the PAPILIONIDAE. (1) The quantity of these pigments is much smaller, so that they are far more difficult to detect, whereas in most of the other instances they are abundant and easily demonstrated. (2) They are often present in some forms only of each species. This is entirely different from anything encountered elsewhere, except in *Graphium ariarathes* Esp. and *G. lysithous* Hb. (p. 81). In consequence of these two considerations, the existence of anthoxanthins in the genus *Polydorus* is very easily overlooked. In writing on this subject on a previous occasion (Ford, 1938a) I was myself completely deceived. For at that time I had an insufficient acquaintance with the American species, among which alone are traces of these pigments to be found—usually in certain forms only.

If anthoxanthins occur in any form of a species, it is listed as possessing them in Tables 6 and 9. It should be noticed that this tends to exaggerate the importance of these pigments in *Polydorus*. Their distribution in the species of this genus is examined more fully in Table 7. I am, of course, concerned only with those forms possessing white or yellow pigments. These colours are more frequently absent from the males than from the females. However, when they occur in the former sex, no sexual difference in the distribution of anthoxanthins is to be detected. Consequently, the two sexes are not separately distinguished in Table 7. In general, it may be said that anthoxanthins are absent in pure white spots but present in those of a cream or yellowish colour. It is possible that these pigments exist in some of the other species of the Aeneas group in which I have not studied the appropriate forms. Thus I would attach no significance to the distribution within this group of the species recorded as possessing them.

TABLE 6.

Species of the genus *Polydorus* tested for anthoxanthins. Total: 62. These pigments are absent in all but 13, marked *.

Region	Group	Species
Indo-Australian	Nox	<i>priapus</i> Bdv., <i>hageni</i> Rogenh., <i>varuna</i> White, <i>zaleucus</i> Hew., <i>nox</i> Sw.
	Latreillei	<i>latreillei</i> Don., <i>adamsoni</i> Sm., <i>nevilli</i> Wood-Mas., <i>philoxenus</i> Gray, <i>dasarada</i> Moore
	Coon	<i>neptunus</i> Guér., <i>coon</i> F., <i>rhodifer</i> Btl.
	Hector	<i>hector</i> L., <i>jophon</i> Gray, <i>pandiyana</i> Moore, <i>oreon</i> Doh., <i>liris</i> Godt., <i>polyphontes</i> Bdv., <i>polydorus</i> L., <i>aristolochiae</i> F., <i>annae</i> Feld., <i>phegeus</i> Hopff.
African	Antenor	<i>antenor</i> Drury
American	Ascanius	<i>ascanius</i> Cr., <i>agavus</i> Drury,* <i>proneus</i> Hb., <i>chamissonia</i> Esch., <i>phalaecus</i> Hew.
	Aeneas	<i>triopas</i> Godt., <i>chabrias</i> Hew., <i>coelus</i> Bdv., <i>steinbachi</i> Roths., <i>klagesi</i> Ehrm., <i>aeneas</i> L.,* <i>dardanus</i> F.,* <i>sesostris</i> Cr.,* <i>childrenae</i> Gray,* <i>erlaces</i> Gray, <i>cutorina</i> Stgr.,* <i>vertumnus</i> Cr.,* <i>lycimenes</i> Bdv.,* <i>erithalion</i> Bdv.,* <i>iphidamas</i> F.,* <i>anchises</i> L.,* <i>nephalion</i> Godt.*
	Lysander	<i>aglaope</i> Gray, <i>lysander</i> Cr., <i>echemon</i> Hb., <i>neophilus</i> Hb., <i>zacyanthus</i> F., <i>arcas</i> Cr.,* <i>timias</i> Gray.
	Polydamas	<i>philenor</i> L., <i>devilliers</i> Godt., <i>streckerianus</i> Honr., <i>archidamas</i> Bdv., <i>polydamas</i> L., <i>madyes</i> Dbl., <i>belus</i> Cr., <i>laodamas</i> Fldr., <i>crassus</i> Cr.

TABLE 7.

The distribution of anthoxanthins among the forms of the *Polydorus* species possessing them (see Table 6). Only forms with white or yellow markings are considered.

Species	Forms	
	Anthoxanthins	
	absent	present
<i>agavus</i> Drury	—	all
<i>aeneas</i> L.	white-spotted forms (e.g. <i>marcius</i> Hb.)	yellow-spotted forms (e.g. <i>bolivar</i> Hew.)
<i>dardanus</i> F.	—	all
<i>sesostris</i> Cr.	white-spotted forms	yellow-spotted forms
<i>childrenae</i> Gray	—	all
<i>cutorina</i> Stgr.	—	all
<i>vertumnus</i> Cr.	white-spotted forms (e.g. <i>vuracares</i> R. & J.)	yellow-spotted forms (e.g. <i>autumnus</i> Stgr.)
<i>lycimenes</i> Bdv.	most forms (e.g. <i>paralius</i> R. & J.)	<i>erythrus</i> R. & J.
<i>erithalion</i> Bdv.	—	all
<i>iphidamas</i> F.	most forms (e.g. <i>elatos</i> R. & J.)	<i>iphidamas</i> F.
<i>anchises</i> L.	most forms	<i>osiris</i> Feld.
<i>nephalion</i> Godt.	—	all
<i>arcas</i> Cr.	—	all

TABLE 8.

Species of the genus *Graphium* tested for anthoxanthins. Total: 92. All possess these pigments except 10, marked *.

Region	Group	Species
Palaearectic and Indo-Australian	Antiphates	<i>eurous</i> Leech, <i>glycerion</i> Gray, <i>podalirius</i> L.,* <i>alebion</i> Gray, <i>agetes</i> Westw., <i>stratiotes</i> Sm., <i>leosthenes</i> Dbl., <i>nomius</i> Esp., <i>aristeus</i> Cr., <i>rhesus</i> Bdv., <i>dorcus</i> Dehaan, <i>androcles</i> Bdv., <i>antiphates</i> Cr., <i>epaminondas</i> Ob., <i>euphrates</i> Fldr.
	Payeni	<i>gyas</i> Westw.*
	Codrus	<i>macleayanus</i> Leach, <i>weiskei</i> Ribbe, <i>codrus</i> Cr.
	Eurypylus	<i>mendana</i> G. & S., <i>eurypylus</i> L., <i>meyeri</i> Hopff., <i>bathycles</i> Zink., <i>leechi</i> Roths., <i>agamemnon</i> L.
	Macareus	<i>macareus</i> Godt., <i>xenocles</i> Dbl., <i>leucothoe</i> Westw., <i>deleserti</i> Guér., <i>megarus</i> Westw., <i>stratocles</i> Fldr., <i>deucalion</i> Bdv., <i>thule</i> Wall., <i>idaeoides</i> Hew.,* <i>encelades</i> Hew.
African	Pylades	<i>endochus</i> Bdv., <i>pylades</i> F., <i>morania</i> Angas
	Tyndaraeus	<i>cyrnus</i> Bdv.
	Leonidas	<i>leonidas</i> F., <i>levassori</i> Ob., <i>hachei</i> Dew., <i>moebii</i> Suff., <i>auriger</i> Btl., <i>odin</i> Strand, <i>ucalegon</i> Hew., <i>agamedes</i> Westw., <i>adamastor</i> Bdv., <i>almansor</i> Honr., <i>philonoe</i> Ward.
	Policenes	<i>evombar</i> Bdv., <i>antheus</i> Cr., <i>policenes</i> Cr., <i>polistratus</i> Sm., <i>junodi</i> Trim., <i>porthaon</i> Hew.
	Kirbyi	<i>kirbyi</i> Hew.
American	Lysithous	<i>pausanias</i> Hew., <i>protodamas</i> Godt., <i>phaon</i> Bdv., <i>euryleon</i> Hew., <i>harmodius</i> Dbl., <i>trapeza</i> R. & J., <i>xynias</i> Hew., <i>ariarathes</i> Esp., <i>ilius</i> F., <i>branchus</i> Dbl., <i>lysithous</i> Hbn., <i>asius</i> F.*
	Marcellus	<i>marcellus</i> Cr., <i>celadon</i> Luc.,* <i>zonaria</i> Btl.,* <i>philolaus</i> Bdv.,* <i>arcesilaus</i> Luc.,* <i>epidaus</i> Dbl.,* <i>bellerophon</i> Dalm.
	Protesilaus	<i>agesilaus</i> Guer.,* <i>glaucolaus</i> Bates, <i>molops</i> R. & J., <i>protesilaus</i> L., <i>stenodesmus</i> R. & J., <i>telesilaus</i> Fldr.
	Thyastes	<i>dioxippus</i> Hew., <i>lacandones</i> Bates, <i>leucaspis</i> Bates
	Doliceaon	<i>serville</i> Godt., <i>columbus</i> Koll., <i>orabilis</i> Btl., <i>salvini</i> Bates, <i>callias</i> R. & J., <i>doliceaon</i> Cr., <i>iphitas</i> Hbn.

It will be seen from Tables 8 and 9 that, unlike the three preceding genera, *Graphium* contains predominantly species which possess anthoxanthins, generally in abundance. However, they are not always easy to detect in the Macareus group, in which the quantity is small and the scaling of the pale areas often defective. It may be added that *G. auriger* Btl. and *G. odin* Strand provide an example of two closely allied species in which the amount of anthoxanthin differs considerably, being much smaller in the latter.

I have found two *Graphium* species in which anthoxanthins exist in some forms but not in others. (1) They occur in most forms of *G. ariarathes* Esp. (e.g. *luctra* R. & J.), but are absent in *G. a. evagoras* Gray. (2) They are usually present, in very small quantity, in the forms of *G. lysithous* Hbn., but not in *G. l. lysithous* itself. It is a highly remarkable fact that there should exist (here and in *Polydorus*) species in some forms of which anthoxanthins contribute to the white and yellow pigments while in others they do not. It would be of much interest to obtain information on the genetics of this situation.

I have already commented on its significance in respect of *G. ariarathes* (Ford, 1938a, 1940).

According to Cockayne (1924), the only species of *Graphium* (*Cosmodesmus*) which show any considerable fluorescence in ultra-violet light are *G. zonaria* Btl. and *G. philolaus* Bdv. This observation attracted my special attention, since these chance to be two of the exceptional *Graphium* species from which anthoxanthins are absent. In all, these exceptions amount only to 10 out of 92 (Tables 8 and 9). I therefore examined the remainder of them under ultra-violet light. I found that while the fluorescence of the other eight is not always so brilliant as in the species mentioned by Cockayne, it is none the less definite. *Graphium asius* F., *arcesilaus* Luc., *epidarus* Dbl., and *G. agesilaus* Guér., fluoresce brightly, *G. gyas* Westw. and *idaeoides* Hew. do so to a somewhat smaller extent, while the fluorescence of *G. podalirius* L. and *G. lysithous*⁵ is slight but detectable. In *celadon* Luc. the scales are degenerate over the pale areas. However, a single pale spot, distal to the red mark on the upperside of the hind-wings, is normally scaled. This shows no evidence of anthoxanthin pigment, and is fluorescent in ultra-violet light. Anyone who compares simultaneously the behaviour under ultra-violet light of one of these with that of such species as *marcellus* Cr. or *bellerophon* Dalm., which contain abundant anthoxanthins, will be in no doubt of the fluorescence of the former.

The members of the *Protesilaus* group are exceedingly similar in appearance. The absence of anthoxanthins from *G. agesilaus* Guér. on the one hand, and its fluorescence in ultra-violet light on the other, are in equal and surprising contrast with its close allies. The same is true of *G. marcellus* Cr. and *G. bellerophon* Dalm., both being non-fluorescent in ultra-violet light and possessing anthoxanthins, when compared with the other members of the *Marcellus* group.

The relation between the distribution of anthoxanthin pigments and the present classification is indicated by the fact that 7 out of the 10 exceptional species of *Graphium* belong to the *Marcellus* group or to its close allies. Indeed it is noteworthy that the single species of the *Lysithous* group (*G. asius* F.), and the single species of the *Protesilaus* group (*G. agesilaus* Guér.), which are without anthoxanthins should have been placed respectively at the end and the beginning of their groups (Table 8): that is, next to the *Marcellus* group.

Graphium idaeoides Hew., which mimics *Idea leuconoë*, is very distinct from its allies and possesses no anthoxanthin pigment. It should certainly be moved to the end of the *Macareus* group.

In general, it may be said that anthoxanthins contribute to the white and yellow colours of the *Graphium* species, save in a few exceptions in which they appear to be replaced by pale yellow pigments fluorescent in ultra-violet light.

The four genera already discussed comprise the true "Swallowtails." In the *Macrolepidoptera of the World* they were combined in the single immense genus *Papilio*. In that work they are followed by twelve other genera, which complete the family *PAPILIONIDAE*. With the exception of *Parnassius*, these are all small, containing three species or fewer. Table 9 shows the distribution of anthoxanthins within these remaining genera⁶ (as well as within the true Swallowtails). Their order is that followed in the *Macrolepidoptera of the*

⁵ In this species anthoxanthins are present in small quantity only, or are absent (p. 81).

⁶ In several instances, prior generic names must be substituted for those used in the *Macrolepidoptera of the World*, as follows: *Cressida* Sw., 1833 (= *Eurycus* Bdv., 1836); *Lamproptera* Gray, 1832 (= *Leptocircus* Swainson, 1833); *Zerynthia* Ochsenh., 1816 (= *Thais* F., 1807; preoccupied for a Molluscan genus, *teste* Bryk, 1922).

TABLE 9.

The occurrence of anthoxanthins in the genera and species of the family PAPILIONIDAE.
(* = approximate only.)

Genus	Species			
	Anthoxanthins		Total examined	Total in genus
	present	absent		
<i>Papilio</i>	—	116	116	?
<i>Troides</i>	—	19	19	27 *
<i>Polydorus</i>				
(Old World)	—	(24)	(24)	?
(New World)	(13)	(25)	(38)	?
Total	13	49	62	?
<i>Graphium</i>	82	10	92	?
<i>Euryades</i>	—	2	2	2
<i>Baronia</i>	—	[1]	1	1
<i>Cressida</i>	—	1	1	1
<i>Lamproptera</i>	2	—	2	2
<i>Teinopalpus</i>	—	1	1	1
<i>Luehdorfia</i>	—	1	1	1
<i>Bhutanitis</i>	—	2	2	3
<i>Sericinus</i>	—	1	1	1
<i>Zerynthia</i>	—	3	3	3
<i>Hypermnestra</i>	—	1	1	1
<i>Doritis</i>	—	1	1	1
<i>Parnassius</i>	29	—	29	29 *

World, as far as can be determined by combining the accounts of the different faunistic regions. In the next paper of this series additional information on the chemistry of these genera can be combined with the data here provided. It will then be possible to relate these additional genera to the various groups of the true Swallowtails to which they are allied. The order now followed will therefore be greatly altered, resulting, it is hoped, in a more natural classification of the PAPILIONIDAE.

It will only be necessary here to comment on a few special points. Owing to the great rarity of the single species of *Baronia* (*B. brevicornis* Salvin), it has not been possible to sacrifice specimens for pigment extraction. The yellow areas are of a deep shade which would make the ammonia test for anthoxanthins effective only if the amount present were considerable. No alteration can be detected on fuming, and general considerations suggest that this genus is related to those *Aristolochia* butterflies in which anthoxanthins are absent. The point can of course be established when sufficient material becomes available for pigment extraction from, say, 6 specimens.

The two species of *Bhutanitis* Atkinson 1873 (= *Armandia* Blanch., 1871 praeocc.) which have been studied are of course *thaidina* Blanch. and *lidderdalei* Atkinson. Very few specimens of *mansfieldi* Riley are known.

Since I have examined approximately the whole of the *Parnassius* species⁷ and have encountered no exceptions, it appears unnecessary to list them. The presence of anthoxanthin pigment is clearly a fundamental character of the genus.

⁷ Some doubt exists as to the specific status of certain forms.

On fuming all species of *Parnassius* with ammonia, several seconds elapse before any reaction is obtained; the resulting yellow coloration then remains for some minutes after exposure. I have never encountered such a delay elsewhere. It seems due to the heavy chitination of the scales, rather than to the quality of the anthoxanthins themselves. This is strongly indicated by the fact that a similar delay occurs in the reaction of the quite unrelated red pigment of this genus. It is of the type converted to yellow by an acid and subsequently reconvertible to red by ammonia (see Ford, 1937, 1940). On extracting with ethyl acetate, 6 specimens of *P. apollo* L. supply sufficient anthoxanthin pigment to produce a positive reaction, while 3 do not. The amount available is therefore less than in the Pierine genus *Enantia* (p. 76), though the latter are much smaller butterflies. The deep colour obtained on fuming with ammonia suggests that this is due to the thin scaling of *Parnassius*, and that the amount of pigment within each scale is considerable.

In *Lamproptera* (= *Leptocircus*) the presence of anthoxanthins is demonstrated easily in *L. curius* F., but with some difficulty in *L. meges* Zink. The oblique band crossing the wings in the former species is coloured white by a pigment containing anthoxanthins enclosed within normal scales. In the latter, this band is scaleless and its colour is produced by a pale green inter-laminar pigment. The only region available for anthoxanthins is the narrow white outer edge of the hind-wings and tails, and here they can be detected.

I have already pointed out (Ford, 1938a) that the presence of anthoxanthins in *Lamproptera* (*Leptocircus*) supports the suggestion of Jordan (1908-9: 107) that this genus is derived from *Graphium* (*Cosmodesmus*). At that time I had not discovered traces of anthoxanthin pigment in some of the American species of *Polydorus*, but I see no reason to modify my previous view on that account. *Graphium* remains the only genus of true "Swallowtails" of which anthoxanthin pigments are characteristic. *Lamproptera* is an Oriental genus, while anthoxanthins are absent from the Old World species of *Polydorus*, as they are throughout *Troides* and *Papilio* s.s. Consequently, the existence of anthoxanthins in *Lamproptera* provides strong support for its affinity with *Graphium*, a conclusion originally reached on quite other grounds.

5. The occurrence of anthoxanthins in other families.

As already explained (p. 69), I have made a brief survey of the distribution of anthoxanthins in the remaining families of butterflies and in a selection of the families of moths, so that those working on any of them may know if the occurrence of these pigments provided them with an additional character for taxonomic study. The results are given in Tables 10 and 11. These list the total number of genera examined possessing white or yellowish colours, and the number of these to which anthoxanthins either do or do not contribute. The genera chosen have been selected as widely as possible through each family. In order to save very extensive tabulations, only those are given in which these pigments have been found. Representative species only have been selected within each, but a considerable number have been studied within all the larger genera. Their behaviour has been consistent within each genus except where stated to the contrary.

It has been my aim to show in which families anthoxanthins exist. However, I have worked out their dispersal in the SATYRIDAE in a little more detail, in order to demonstrate that the occurrence of these pigments can be made to give information of some value on classification even when investigated less extensively than has been done in the PIERIDAE and PAPILIONIDAE.

The distribution of anthoxanthins within the various families of butterflies is given in Table 10. The nomenclature is based on that of the *Macrolepidoptera of the World*. The PAPILIONIDAE and PIERIDAE, already discussed, are added here for the sake of completeness in comparison. It will be necessary to mention only a few points of importance in regard to each.

In the DANAIDAE the number both of genera and species is remarkably small considering the importance of the family. I have tested several species

TABLE 10.

The occurrence of genera possessing anthoxanthins within the families of the Rhopalocera. Subfamilies are added when of special importance. In the PAPILIONIDAE and the PIERIDAE every existing genus has been tested. (* = these contain a single genus only).⁸

Family	Genera			
	Anthoxanthins		Total examined	Per cent. possessing anthoxanthins
	present	absent		
PAPILIONIDAE	4	12	16	25
PIERIDAE	5	63	68	7
DANAIDAE				
(ITHOMINAE)	—	(8)	(8)	—
(DANAINAE)	—	(11)	(11)	—
Total	—	19	19	—
SATYRIDAE	7	39	46	15
AMATHUSIIDAE	—	6	6	—
BRASSOLIDAE	—	4	4	—
MORPHIDAE	—	1	1 *	—
NYMPHALIDAE				
(ACRAEINAE)	—	(3)	(3)	—
(HELICONINAE)	—	(1)	(1)	—
(NYMPHALINAE)	—	(88)	(88)	—
Total	—	92	92	—
ERYCINIDAE				
(LIBYTHEINAE)	—	(1)	(1) *	—
(RIODININAE)	(3)	(21)	(25)	(12)
Total	3	22	26	12
LYCAENIDAE	6	19	25	24
HESPERIIDAE	10	15	25	40

within all the larger genera (*Danaus*, *Amauris*, *Euploea*), making sure that they are widely separated within them.

I have examined the SATYRIDAE in some detail. The seven genera possessing anthoxanthins (out of 46 tested) are as follows: *Arge* (12 species tested, present in all), *Satyrus* (present in *circe* F., *briseis* L., *prieuri* Pierret, *anthe* Ochs, *sybillina* Ob.; absent in *hermione* L., *alcyone* Schiff.), *Aulocera* (*brahminus* Blanch., *swaha* Koll., *padma* Koll., *saraswati* Koll.), *Oeneis* (present in *aello* Hbn., *tarpeia* Pall., absent in 6 other species), *Physcaeneura* (*leda* Gerst.), *Coenonympha* (19 species tested, present in all), *Oressinoma* (*typhla* D. & H.). In the first six of these genera the anthoxanthins are abundant; in the last they are present in small quantity only.

⁸ The arrangement of the *Macrolepidoptera of the World* is followed in this table. However, the name ERYCINIDAE is now replaced by RIODINIDAE, and the Libytheini are included in the NYMPHALIDAE.

Seitz (1908) placed *Arge*, *Oeneis*, and *Satyrus* consecutively, while Fruhstorfer (1911) reversed the order of the last two. Seitz actually included the *Aulocera* species in *Satyrus*, while Fruhstorfer separated them by two small genera, *Orinoma* (without anthoxanthins) and *Rhaphicera* (not examined). Chemical evidence suggests that *Aulocera* and *Satyrus* should at least be placed next to each other. Aurivillius (1911) separated *Physcaeneura* from *Satyrus* (called by him *Pararge*) by four small genera: *Leptoneura*, *Meneris*, and *Aphysoneura* (all without anthoxanthins), and *Coenyra* (not tested). This separation is probably an error.

Coenonympha is far removed from the genera just discussed; but Weymer (1910, 1911, 1912) separated *Oressinoma* from it only by two monospecific genera, *Paramecera* (without anthoxanthins) and *Satyrodes* (not examined). *Coenonympha* and *Oressinoma* should perhaps be brought together.

TABLE 11.

The occurrence of genera possessing anthoxanthins within certain families of the Heterocera.

Family	Genus			
	Anthoxanthins		Total examined	Per cent. possessing anthoxanthins
	present	absent		
SPHINGIDAE	1	11	12	8
NOTODONTIDAE	—	5	5	—
GEOMETRIDAE	—	50	50	—
SATURNIIDAE	—	7	7	—
URANIIDAE	—	5	5	—
SYNTOMIDAE	—	4	4	—
ARCTIDAE	—	14	14	—
AGARISTIDAE	5	6	11	45
AGROTIDAE	1	52	53	2
LYMANTRIDAE	—	13	13	—
HYPSIDAE	—	9	9	—
ZYGAENIDAE	3	5	8	38
CASTNIDAE	—	1	1	—

It will thus be seen that two distinct groups of genera in the SATYRIDAE possess anthoxanthins. These centre round *Arge* and *Coenonympha*. Consequently the distribution of these pigments is rather closely related to the present classification of the family.

The AMATHUSIIDAE and BRASSOLIDAE contain only 15 and 8 genera respectively. In the latter family is a large genus *Caligo*, of which I have examined four species. The MORPHIDAE comprise the single genus *Morpho*, within which I have also examined four species.

The subfamily ACRAEINAE of the NYMPHALIDAE includes the very large genus *Acraea*; here I have tested 16 species. Within the HELICONIINAE I have examined 8 species of *Heliconius*. In the vast subfamily NYMPHALINAE I have examined several species within the larger of the 88 genera studied.

It appears, therefore, that anthoxanthins are absent from the great family NYMPHALIDAE. I have based this conclusion upon the study of a large number of the genera because it is always difficult to establish a negative proposition.

However, these pigments are found in the three families remaining to be mentioned. I have accordingly examined a sample of 25 genera scattered as widely as possible within each, in order to give a rough indication of frequency. In the ERYCINIDAE this sample is in addition to the very distinct genus *Libythea*.

The 3 genera of the ERYCINIDAE in which I have found anthoxanthins are *Helicopsis*, *Calydna*, and *Anteros*. I have found these pigments in the following genera of LYCAENIDAE: *Phlyaria*, *Castalius* (in some species they are present, in others absent), *Lycaenopsis*, *Thysonotis*, *Talicada*, *Nacaduba*.

Table 10 shows that anthoxanthins are especially common in the HESPERIIDAE. I have found them in the following genera: *Hesperia*, *Hyalothyris*, *Pellicia*, *Udaspes*, *Heliopetes*, *Milanion*, *Baracus*, *Netrobalane*, *Gomalia*, *Abantis*. In the last genus they are absent from *A. venosa* Trim., *A. paradisea* Btl., *A. zambesiaca* Westw., *A. bismarcki* Karsch., and present in *A. tettensis* Hopff., and *A. levebu* Wallengr. It may be questioned whether these two species should not be separated from *Abantis* (not necessarily into the same genus). This plan has already been advanced in favour of *levebu*, which is sometimes given a genus *Leucochitonea* Wallengr. It appears, therefore, that anthoxanthins are widely distributed in the HESPERIIDAE, a fortunate circumstance in a family of notorious taxonomic difficulty, where an additional character for study may be welcome.

Table 11 shows the distribution of anthoxanthins within a number of families of the Heterocera. The genera in which I have found them are as follows: SPHINGIDAE, the single American genus *Euproserpinus* (*E. phaeton* Gr. & Rob., a day-flying form). In the AGARISTIDAE, when present, the quantity is small. They occur in *Rothia*, *Charilina*, *Aegocera*, *Paraegocera*, and *Hespagarista*.

It is clear that anthoxanthins must be very rare in the great family AGROTIDAE (NOCTUIDAE). I have found them in a single genus only (out of 53), namely *Apsarasa* (*A. radians* Westw.). It belongs to the subfamily ACRONICTINAE, and Mr. W. H. T. Tams kindly informs me that he does not regard it as in any way exceptional. In the ZYGAEINIDAE I have detected these pigments in *Chalcusia* (3 species tested, present in all), *Cyclosia* (present in *C. papilionaris* Drury and *C. pieroides* Walker, absent in *C. macularia* Guér. and *C. pieridoides* H.-S.) and *Caffricola*.

It seems that anthoxanthins are absent from, or very rare in, the vast family GEOMETRIDAE, since I have tested a sample of 50 widely scattered genera without detecting them. Yet white pigments are exceedingly common among the species.

In general, a comparison of Tables 10 and 11 suggests that anthoxanthins are more frequent in the butterflies than in the moths. They occur in 7 out of 11 families in the former, and in 4 out of 13 in the latter; that is, twice as commonly in the butterflies.⁹ A peculiar circumstance also is their apparent association with day-flying forms since, out of 10 genera of moths in which I have found them, only 1 (*Apsarasa*) is probably nocturnal.

It would be a delightful task to study the distribution of these pigments relative to classification in the remaining families of butterflies, and in the moths, in which they are known to occur. I must leave this, as I hope, for others, since I have now devoted as much time to this subject as I can spare.

⁹ An almost equal disparity is obtained when the number of genera tested is considered. The result is 38 out of 328 in the butterflies and 10 out of 192 in the moths. Thus again anthoxanthins occur twice as commonly in the former group. However, such estimates are very rough, owing to unequal sampling.

6. Summary.

1. It is proposed to publish a short series of papers on the chemistry of wing-pigments in the Lepidoptera with reference to their bearing on classification. Of these the present work, devoted to the anthoxanthins, is the first.

2. Anthoxanthins are plant pigments responsible for a series of colours from white to yellow. In general, they are very rare in animals, which cannot manufacture them but derive them from their food.

3. So far, they have been reported in the Lepidoptera in one or two instances only, for the white and yellow pigments of this Order are usually of a different nature.

4. It is here shown that, though uncommon, anthoxanthins are widely spread in the Lepidoptera. When they occur, they are generally not alone responsible for white and yellow colours, other pigments being present in addition.

5. Their existence has been demonstrated by the tests described on p. 68.

6. The distribution of anthoxanthins has been studied in detail in the PIERIDAE and the PAPILIONIDAE. A less thorough survey has been made of their occurrence in the other families of butterflies, and in a number of families of moths, so that taxonomists will know where they are available for use.

7. Anthoxanthins are very rare in the PIERIDAE, but are found in the aberrant central and South American family DISMORPHIINAE (in the genus *Dismorphia* in 12 out of 50 species tested, and in all three species of *Pseudopieris*).

8. They also occur in all three species of the Palaearctic "Wood Whites" (*Leptidea*), which have been united with the DISMORPHIINAE on structural grounds. Their presence supplies independent evidence for this affinity.

9. The 12 species possessing anthoxanthins in the large genus *Dismorphia* are not distributed at random on the existing classification but (except for the interpolation of *thermesia* Godt.) they are all grouped together.

10. They form a compact assemblage, now to be separated from *Dismorphia* as the genus *Enantia*.

11. The absence of anthoxanthins in *thermesia* Godt. indicated that this species had been misplaced. On further investigation, this conclusion proved to be supported on structural evidence.

12. The distribution of anthoxanthins supplies a natural order for the genera of the DISMORPHIINAE (p. 76).

13. Outside the DISMORPHIINAE, anthoxanthins are almost non-existent in the PIERIDAE, occurring only in 2 out of 233 species tested. In one of these, *Eronia cleodora* Hbn., the amount is so small as to be nearly undetectable. In the other, *Gandaca harina* Horsf., it is large.

14. Chemical evidence, therefore, confirms the view that the mono-specific genus *Gandaca* is an isolated one, not closely related to *Eurema*, with which it was formerly associated.

15. It is possible that the possession by *Gandaca* of abundant anthoxanthins indicates some affinity with *Leptidea* in the DISMORPHIINAE. If so, the COLLADINAE, feeding on Leguminosae, to which *Gandaca* belongs, should be placed next to that family. *Leptidea* also feeds on Leguminosae, though the PIERINAE and TERACOLINAE feed on Cruciferae and Capparidaceae respectively.

16. In the PAPILIONIDAE anthoxanthins are found in 4 genera out of 16.

17. They are present in *Polydorus* in small quantity and in some American species only. Their distribution can be employed to adjust the species to a more natural order.

18. They are found in all the species of *Graphium* tested except 10 (out of 92), in which they appear to be replaced by a pale yellow pigment fluorescent in ultra-violet light. The distribution of the exceptions is related to classification.

19. Anthoxanthins are present in both species of *Lamproptera*, so confirming their suggested affinity with *Graphium*.

20. In a few instances, one form of a species may possess anthoxanthins and another not. The significance of this is discussed.

21. Anthoxanthin pigments are found also throughout *Parnassius*.

22. The distribution of anthoxanthins within the PAPILIONIDAE will be more fully related to classification in a subsequent paper, in which the red pigments can be considered in addition.

23. The distribution of anthoxanthins in other families of butterflies is given in Table 10. This represents a general survey only, except for the SATYRIDAE, which have been studied somewhat more fully.

24. In the latter family, anthoxanthins are found in genera grouped round *Arge* and *Coenonympha* respectively.

25. Table 24 shows the distribution of anthoxanthins in certain families of moths.

26. In general, the occurrence of anthoxanthins within the Lepidoptera supports the present classification of the Order upon evidence wholly distinct from that upon which it had been constructed. It further provides a useful addition to the characters available for taxonomic study, from which results of some value have already been obtained.

7. REFERENCES.

- AURIVILLIUS, C., 1908, 1910, in Seitz, *The Macrolepidoptera of the World*, Africa (PAPILIONIDAE) **13** : 11-28.
 —, 1911, *ibid.* (SATYRIDAE) **13** : 81-119.
 BAYLIS, H. A., 1924, *Entomologist* **57** : 2-6.
 BRYK, F., 1923-30, *Lepidopterorum Catalogus* **24** : 676.
 COCKAYNE, E. A., 1924, *Trans. ent. Soc. Lond.* **1924** : 1-19.
 FORD, E. B., 1937, *Biol. Rev.* **12** : 461-503.
 —, 1938a, *The Genetic Basis of Adaptation*, in *Evolution*, Oxford.
 —, 1938b, *The Study of Heredity*, London.
 —, 1940, *Ann. Eugen.* **10** : 227-52.
 FRUHSTORFER, H., 1911, in Seitz, *The Macrolepidoptera of the World*, Indo-Australia (SATYRIDAE) **9** : 285-401. (Stuttgart.)
 GEROULD, J. H., 1921, *J. exp. Zool.* **34** : 385-412.
 HOPKINS, F. G., 1895, *Trans. Roy. Soc. Lond. (B)* **186** : 661-82.
 IMMS, A. D., 1937, *Recent Advances in Entomology*, 2nd edit.
 JORDAN, K., 1907, in Seitz, *The Macrolepidoptera of the World*, America (PAPILIONIDAE) **5** : 11-45. (Stuttgart.)
 —, 1908-9, *ibid.*, Indo-Australia **9** : 11-109.
 MANUNTA, C., 1935, *Mem. Acad. Naz. Lincei*, (6) **6** : 75-161.
 RÖBER, J., 1907-8, in Seitz, *The Macrolepidoptera of the World*, Palaearctic Region (PIERIDAE) **1** : 39-74. (Stuttgart.)
 —, 1909, *ibid.*, America **5** : 53-111.
 SCHÖPF, C., and BECKER, E., 1933, *Liebig's Ann.* **507** : 266-96.
 SCOTT-MONCRIEFF, R., 1936, *J. Genet.* **32** : 117-70.
 SEITZ, A., 1907, *The Macrolepidoptera of the World*, Palaearctic Region (PAPILIONIDAE) **1** : 7-19. (Stuttgart.)
 —, 1908, *ibid.* (SATYRIDAE) **1** : 114-53.

- TALBOT, G., 1932-35, *Lepidopterorum Catalogus* 23 (Parts 53, 60, 66) : 1-697. (Berlin.)
—, 1939, *The Fauna of British India, Butterflies* 1, 2nd edit.
THOMSON, D. L., 1926a, *Biochem. J.* 20 : 73-5.
—, 1926b, *ibid.* 20 : 1026-27.
VERNE, J., 1930, *Couleurs et Pigments des Êtres vivants*.
WEYMER, G., 1910, 1911, 1912, in Seitz, *The Macrolepidoptera of the World, America* (SATYRIDAE) 5 : 173-283. (Stuttgart.)
WIELAND, H., METZGER, H., SCHÖPF, C., and BÜLOW, M., 1933, *Liebig's Ann.* 507 : 226-65.
WIGGLESWORTH, V. B., 1939, *The Principles of Insect Physiology*.

BOOK NOTICE.

French-English Science Dictionary for Students in Agricultural, Biological, and Physical Sciences. By L. De VRIES. 8vo. London (McGraw-Hill Publishing Co., Ltd.), 1940. Price 24s. 6d. pp. viii + 546, printed in double column.

This Dictionary has been produced by Prof. De Vries with the collaboration of members of the Graduate Faculty of Iowa State College.

It contains some 43,000 entries, is compact in size and in a serviceable flexible binding. Entomology is well covered in the dictionary and special care has been given to include many of the present, past, and future tenses of the irregular verbs which may be a difficulty to the average user of a French-English Dictionary. Past participles and the infinitive form are also given and some 500 common idioms are included.

Many words which are spelled the same in French and English are included in an attempt to assist the reader. It is apparent that the Dictionary has been compiled with the aim of assisting the reader always kept well in mind.

No comprehensive inclusion of names of animals, insects, plants and chemical compounds are attempted owing to limitation of space.

A very useful 12-page list of abbreviations with their English meanings is added to the volume.

A NOTE ON OVIPOSITION PREFERENCES IN *SMERINTHUS POPULI* (L.) (LEPIDOPTERA, SPHINGIDAE)

By J. A. REID, B.Sc., A.R.C.S., F.R.E.S.

THE following is an account of a few very simple experiments made with a single female of the poplar hawk moth, *Smerinthus populi* (L.). It would be exceedingly rash to assume that the results obtained with this specimen are true for the species as a whole, and no such claim is made. It is thought worth while to record the results, because they show that the experimental method employed, though very simple, was nevertheless able to reveal definite oviposition preferences in the insect.

The moth was taken mating on a fence at Gerrards Cross, Buckinghamshire, 28.v.1939. The pair of moths was placed in a tin, and during the night of 28th, 69 eggs were laid. The first experiment was made during the night of 29th. The female moth was placed in a large glass jar about one foot high and eight inches in diameter, closed by a glass lid arranged to allow ventilation. About one inch of damp sand was placed in the bottom of the jar, and single leafy sprigs of willow, sallow and white poplar were stuck into the sand. The following morning the numbers of eggs laid on the different plants were counted. The same method was adopted on subsequent nights, varying the species of plants offered, and the combinations in which they were offered. The following results were obtained :—

Exp. No.	Date	White Poplar	Willow	Sallow	Not on plants	Total
Exp. No. 1.	29 May.	15	0	0	10	25
Exp. No. 2.	30 May.	Aspen	Balsam Poplar	Dwarf Sallow		
	No. of eggs laid .	12	11	0	38	61
Exp. No. 3.	31 May.	Birch	Willow	Sallow		
	No. of eggs laid .	12	9	13	0	34
Exp. No. 4.	1 June.	White Poplar	Balsam Poplar	Aspen	Sallow	
	No. of eggs laid .	21	0	1	0	22
Exp. No. 5.	2 June.	White Poplar	Balsam Poplar	Aspen	Sallow	
	No. of eggs laid .	7	0	6	2	15
Exp. No. 6.	3 and 4 June.	White Poplar	Balsam Poplar	Aspen	Sallow	
	No. of eggs laid .	9	19	0	3	31
Exp. No. 7.	5 June.	White Poplar	Aspen			
	No. of eggs laid .	1	0		3	4
					52	193

When these figures are analysed the following facts emerge. In the course of the experiments 193 eggs were laid, and of these 141, or 72·5%, were laid on the plants. In the second experiment 38 eggs were not laid on the plants, and on this occasion the glass lid was replaced by muslin stretched over the top of the jar, on which 21 of the 38 eggs were laid. This suggests that in experiments of this sort, the insect is probably best confined in some container, such as a glass jar, which presents no rough surface.

In experiments 1, 2, 4, 5, and 6 species of poplar and willow were offered simultaneously (see table below). In these five experiments 101 eggs were laid on species of *Populus* (white, and balsam poplar, and aspen) and only 5 eggs on species of *Salix* (sallow, dwarf willow and willow). Correcting for the fact that the species of *Populus* were offered 12 times and the species of *Salix* only 6 times, there were 50 eggs on *Populus* spp. to 5 on *Salix* spp.; a ratio of 10 : 1. That is to say, the moth showed a strong preference for ovipositing on species of *Populus* rather than on species of *Salix*.

Table summarising the results of the experiments.

Experiment	White Poplar	Balsam Poplar	Aspen	Total <i>Populus</i>	Sallow	Dwarf Sallow	Willow	Total <i>Salix</i>	Birch
1	15	—	—	15	0	—	0	0	—
2	—	11	12	23	—	0	—	0	—
3	—	—	—	—	13	—	9	22	12
4	21	0	1	22	0	—	—	0	—
5	7	0	6	13	2	—	—	2	—
6	9	19	0	28	3	—	—	3	—
7	1	—	0	1	—	—	—	—	—
Totals .	53	30	19	102	18	0	9	27	12

If the species of *Populus* are compared individually with those of *Salix* considered together, it may be seen that 52 eggs were laid on white poplar to 5 on *Salix* (Exps. 1, 4, 5, 6) and this does not allow for the fact that the *Salix* were offered five times and the white poplar four. Similarly (Exps. 2, 4, 5, 6) 30 eggs were laid on balsam poplar to 5 on *Salix*, and 19 on aspen to 5 on *Salix* (Exps. 2, 4, 5, 6).

When the three species of poplar are compared, it is fairly obvious that the moth preferred the white poplar; 37 eggs were laid on it to 19 on balsam poplar (Exps. 4, 5, 6), and while 7 eggs were laid on aspen in the presence of white poplar (Exps. 4, 5, 6, 7), 38 eggs were laid on the latter. It is impossible to say from the results of experiments 2, 4, 5, and 6, whether balsam poplar was preferred to aspen, or the reverse; for though 30 eggs were laid on balsam poplar to 19 on aspen, the balsam poplar was refused in two out of the four experiments and only had more eggs than the aspen once, whilst the latter was only refused in one of the four experiments.

Experiment No. 3 was made to see what would happen if plants that were presumed to be unattractive were offered; it will be seen that the three plants, willow, willow and birch, received approximately equal numbers of eggs.

The moth was found dead on 6 June; it was dissected and the ovaries examined, when 6 fully formed eggs were found in the left ovary and 7 in the right; no semi-mature eggs were seen. The insect laid a total of 263 eggs.

To sum up: when a single female of *Smerinthus populi* (L.) was offered a choice of species of *Salix* and species of *Populus* on which to oviposit, it showed a strong preference for the *Populus*. This agrees with my experience of the species on Gerrards Cross Common, where aspen and willow grow mixed together; I have only found the larvae of *S. populi* on the aspen; larvae on willow have always been those of *S. ocellatus* L. Three species of *Populus* were offered, white poplar, balsam poplar and aspen, and of these white poplar was preferred; in addition to receiving the most eggs, the white poplar was the only species that was not refused on any occasion that it was offered.

THE LARVA AND PUPA OF *TACHINUS SUBTERRANEUS* (LINNAEUS) (COLEOPTERA, STAPHYLINIDAE)

By H. E. HINTON, Ph.D., F.R.E.S.

(Department of Entomology, British Museum (Natural History)).

WITH 15 TEXT-FIGURES.

WHILE collecting during the winter of 1940-41 (1.xii.1940-23.iii.1941) large numbers of larvae and adults of *Tachinus subterraneus* were taken in a compost heap in the grounds of Linton Village College, Cambridgeshire. This heap more or less fills a pit in the ground about ten feet square and three feet deep. During winter it was filled mostly with cabbage leaves. The larvae and adults were found usually near the bottom of the heap among the decayed and partly liquefied cabbage leaves and other plant refuse. Both stages were also collected in other localities near Linton under rotten potatoes, cabbages, etc., on the surface of the ground. The mature larvae were frequently found in small cells in the earth. These cells were usually about six inches from the vertical face of the pit and often two feet below the ground-level. No pupae were seen, but one larva pupated in the laboratory on 27 January, and the adult emerged on 10 February.¹

T. subterraneus appears to be a mid-winter species. Many days were spent collecting in the same compost heap in the summer of 1940, but not a single adult or larva was found. This species, like the vast majority of the STAPHYLINIDAE, is carnivorous, and the adults and larvae appeared to be feeding mainly on dipterous larvae. In captivity they readily attacked and ate each other.

The larvae of seven species of *Tachinus* have been described; two from North America and five from Europe. Four of these occur in England, *T. laticollis* Gravenhorst (1802), *T. humeralis* Gravenhorst (1802), *T. subterraneus* (Linnaeus) (1758), and *T. rufipes* De Geer (1774). The descriptions of *T. laticollis* (Rey, 1892; Xamheu, 1910) and *T. humeralis* (Perris, 1846; Xamheu, 1910) are very poor; and it is only with considerable hesitation that I include them in the key given below. *T. subterraneus* has only been briefly described before now (Rey, 1882; Xamheu, 1910). Schjødte (1872) has given a good description and excellent figures of *T. rufipes*, and I have examined a specimen of the latter in the British Museum and one collected by myself (ii.1941) in a wood near Linton under a decayed piece of *Polyporus squamosus*.

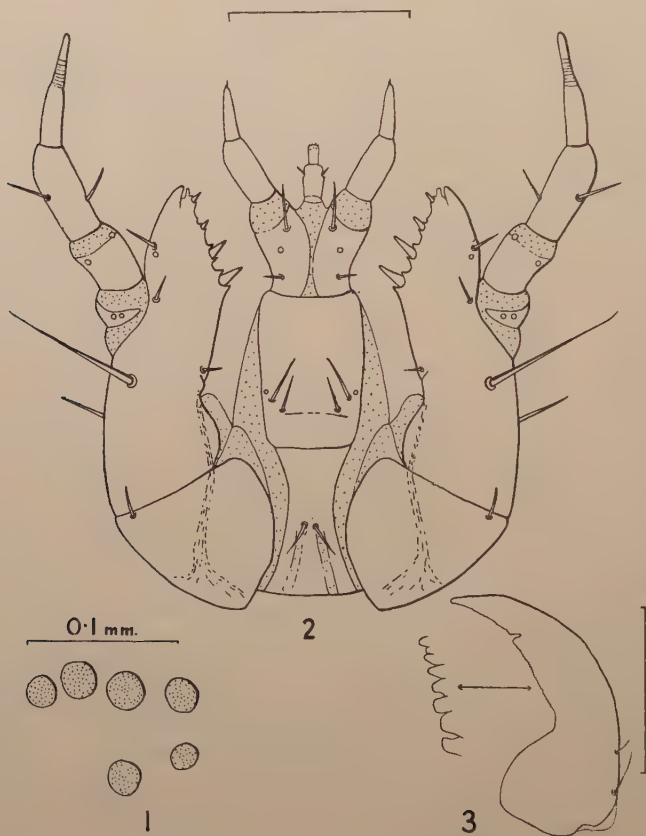
A key to the mature larvae of British *Tachinus*.

1. Length, 6-7 mm. *T. laticollis* Grav., *T. humeralis* Grav.
- Length, 9-10 mm. 2.
2. Length, 9 mm. Front of labrum (fig. 7) on each side near middle without teeth. Mandible (fig. 3) with a narrow incision on cutting edge near apical fourth, without a distinct tooth here. Thoracic tergites (fig. 8) with a

¹ The average laboratory temperature during this time was 68° F. \pm 1, with a minimum of 63° F. and a maximum of 72° F.

single long seta on each side near base (the lateral seta of metanotum is more or less opposite basal seta). First eight abdominal tergites (all similar to first, fig. 8) with transverse row of setae on each side consisting of only two long setae; sides of these tergites with a few very fine, short, and inconspicuous setae. Urogomphi (fig. 6) with second segment considerably less than half as long as first. Abdominal sternites (fig. 10) two to eight with a very fine and inconspicuous seta between second and third, counting from middle outwards, of posterior row; ninth sternite with posterior row consisting of two long setae on each side of middle

T. subterraneus (L.).



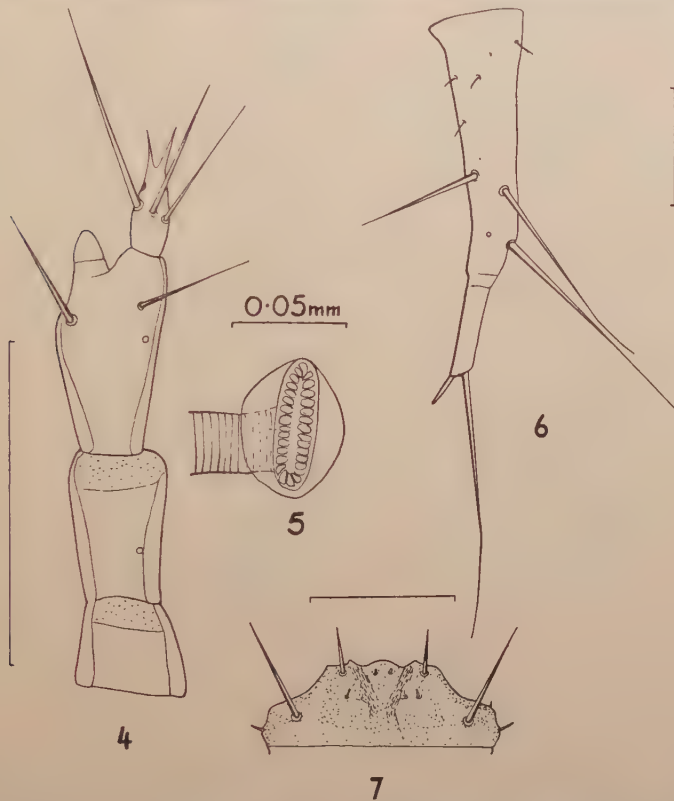
FIGS. 1-3.—Larva of *T. subterraneus* (L.). (1) Ocelli of left side of head. (2) Ventral view of maxilla and labium. (3) Dorsal view of right mandible.

—, Length, 10 mm. Front of labrum on each side near middle with a short but conspicuous, stout tooth. Mandible with a moderately large, stout, and distinct tooth on cutting edge near apical fourth. Thoracic tergites with two long setae on each side near base. First eight abdominal tergites with transverse row of setae on each side consisting of three long and one slightly shorter seta; sides of these tergites with three to four stout, moderately long, conspicuous setae. Urogomphi with second segment considerably more than half as long as first (0.65 mm. : 0.82 mm.). Abdominal sternites two to eight with third seta, counting from middle, of posterior row

nearly as long and stout as others of row; ninth sternite with posterior row consisting of three long, stout, lateral and one distinctly finer, shorter, submedian seta on each side *T. rufipes* De G.

Description of larva of *T. subterraneus* (L.).

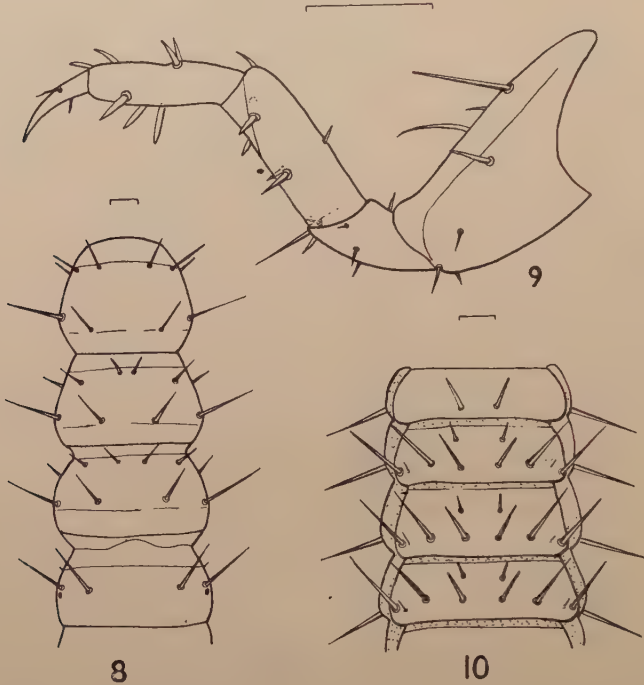
Mature larva: Length, 9 mm.; breadth (across first abdominal segment), 1.2 mm. Body elongate, parallel, and cylindrical to subcylindrical. Cuticle moderately pale brownish-testaceous; pleura and intersegmental membranous areas white to pale yellowish-white. *Head* slightly longer than broad (0.71 mm. : 0.68 mm.); posterior margin broadly, moderately deeply, and arcuately sinuate at middle; coronal suture slightly more than



FIGS. 4-7.—Larva of *T. subterraneus* (L.). (4) Dorsal view of right antenna. (5) Spiracle of fifth abdominal segment. (6) Dorsal view of right urogomphus. (7) Dorsal view of labrum.

one-third as long as head (0.24 mm. : 0.71 mm.) and frontal sutures meeting posteriorly in a curve so that middle of caudal margin of frons is evenly and narrowly rounded, not triangular; surface with a long, stout, erect seta on each side slightly posterior to frontal sutures and three shorter, finer setae as follows: one opposite inner base of antenna, one near antero-ventral ocellus, and one near antero-dorsal ocellus; surface also with a few other much shorter and finer setae. Ocelli with six facets on each side as shown in fig. 1. Antenna (fig. 4) as figured. Labrum (fig. 7) without a tooth very near middle on each side; shape and chaetotaxy as figured. Mandible (fig. 2) with cutting edge deeply and narrowly incised near apical fourth and finely but rather unevenly serrate nearly to apex; outer

margin with two setae near base. Maxilla and labium with shape and setae as figured (fig. 2). Pronotum (fig. 8) with a transverse row of six long, erect setae on anterior fifth, with a single sublateral similar seta near caudal fifth, and with a single long, lateral seta near caudal fourth or third; anterior and posterior fifth with cuticle paler in colour and with a semi-granulate microsculpture arranged in close and distinct longitudinal bands. Mesonotum similar to pronotum but with lateral caudal seta placed farther back so that it appears to form part of a row including caudal sublateral seta. Metanotum similar to mesonotum. Abdominal tergites two to eight similar to first (fig. 8); each with a posterior transverse row of four setae, this row being on posterior half or third on first tergite but nearer caudal margin on following tergites so that on



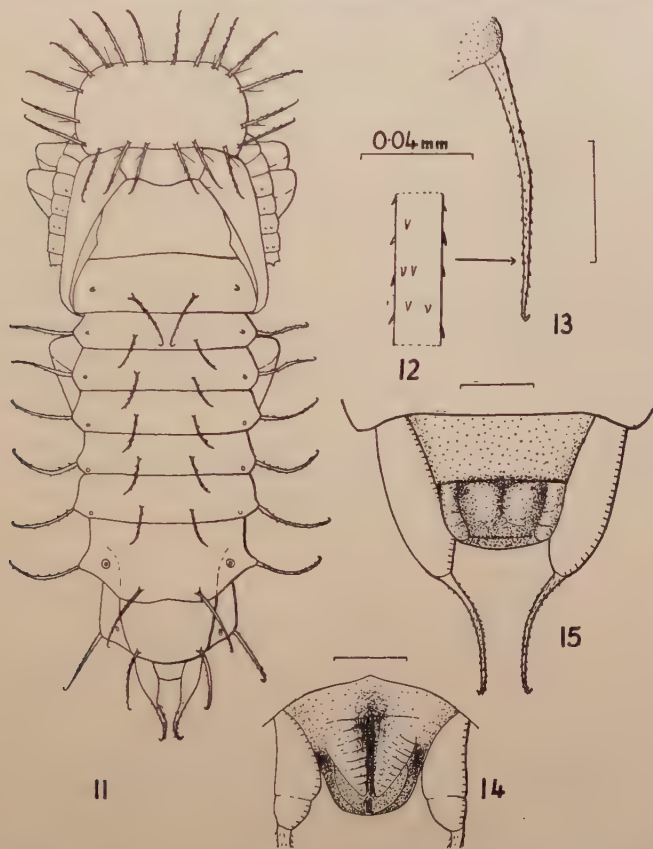
FIGS. 8-10.—Larva of *T. subterraneus* (L.). (8) Dorsal view of thorax and first abdominal segment. (9) Posterior view of left front leg. (10) Ventral view of first four abdominal sternites.

eighth it is on posterior fifth or sixth; sides of tergites with two to three very fine setae; ninth tergite with a single long seta on each side at postero-lateral angle and cuticle without a pale posterior belt. Urogomphi (fig. 6) as figured. Sclerotised part of tenth segment perfectly cylindrical, without pleural and sternal sutures, about as long as ninth tergite, and surface of cuticle with a number of fine, short, erect setae. Pleurites entirely membranous and without setae except for one moderately long, erect seta on anterior middle of mesopleurite anterior to spiracle. Sternite of first abdominal segment with a single caudal seta on each side of middle (fig. 10); sternites two to eight with a single, moderately short, anterior seta on each side of middle and a transverse row of six long setae on posterior fourth or fifth (fig. 11); ninth sternite without extreme lateral seta of posterior row and without the two moderately short anterior setae; on sternites two to eight there is fre-

quently a very fine, short, erect seta near inner base of extreme lateral seta of posterior row. *Legs* all similar in shape and chaetotaxy to front pair (fig. 9) but with hind pair distinctly longer.

Description of pupa of *T. subterraneus* (L.).

Male: Length, 4.5–5.0 mm.; breadth (which is greatest across first abdominal segment when wings are included), 1.7 mm. Body moderately strongly convex; abdomen sub-cylindrical in cross section. Cuticle white and densely, microscopically punctate; without fine hairs but with numerous long, moderately stout, finely spinulose, brownish seta



FIGS. 11–15.—Pupa of *T. subterraneus* (L.). (11) Dorsal view of male. (12) Enlarged portion of a spinulose seta. (13) A typical spinulose seta. (14) Ventral view of apex of female abdomen. (15) Same of male.

(figs. 12 and 13). *Head* completely concealed from above by pronotum. Surface without distinct impressions; on each side near mesal margin of eye with a longitudinal row consisting of three moderately long, erect, spinulose setae and posterior and slightly mesal to eye on each side of vertex with a single similar seta. Antenna extending posteriorly under lateral margin of pronotum and beyond to a point opposite posterior margin of metasternum; apical half of segments with a few low tubercles which become more prominent on five apical segments. *Pronotum* evenly convex and with shape and 20 setae as shown in fig. 11. Mesonotum very short and without setae; elytra extending caudally and slightly ventrally to a point opposite posterior margin of first abdominal segment. Metanotum

long, without impressions and without setae; wings extending caudally and ventrally to a point opposite posterior margin of fourth abdominal sternite. Abdominal tergites with shape and setae as figured (fig. 11); median setae of tergites two to six shorter than others of dorsal surface and with apices not curled over. *Metasternum* with a long, erect, stout, acute tubercle on each side of middle on posterior third of disk. Abdomen without setae on the sternites or at any rate without setae that have not been shown from a dorsal view (fig. 11); apical sternites as shown in fig. 15. *Legs* with all of tibiae and tarsi with numerous low tubercles; front pair with tarsi extending slightly beyond metasternal tubercles and at apex separated by a distance equal nearly to their length; middle legs with tarsi extending to a point opposite posterior margin of first abdominal sternite and separated by a distance equal to their length; hind legs extending slightly beyond posterior margin of fourth abdominal sternite and tarsi nearly contiguous at apex. *Spiracles* of abdomen on dorso-lateral sides of first seven tergites, those of first three opening on short, stout, feebly sclerotised tubercles; eighth segment with spiracles set in a slight depression and opening on middle of pleural membrane.

Female: Externally similar to male but with apical ventral part of abdomen differently formed (cf. figs. 14 and 15) and with two metasternal tubercles only about two-thirds as long.

The single female before me has a short, fine seta on each side of eighth tergite near long submedian seta, but this may be only an individual variation. The fine, moderately long, smooth setae that arise near bases of spinulose setae of the pronotum are often absent on one or more of the spinulose setae in both male and female.

I would here like to express my deep indebtedness to Drs. K. G. Blair and F. van Emden for the encouragement and help that they are always so ready to render in my work on the life-histories of beetles.

BOOK NOTICE.

Entomophagous Insects. By C. P. CLAUSEN. pp. x + 688, 257 figs. 8vo. London (McGraw-Hill), 1940. Price 49s.

This volume is one of the McGraw-Hill Publications in the Zoological Sciences and is uniformly bound with that series.

The book deals with all orders of insects which are known to contain representatives that feed upon other insects and, as is to be expected, the Hymenoptera occupy the greatest place—in fact the first 342 pages are devoted to that Order. After an introductory section the author deals with each Order family by family, describing host preferences; biology and habits; effect of parasitism upon the host; and immature stages.

A long list of references extending to some 50 pages is given and a very extensive index.

“The present volume represents, as nearly as possible, what the author himself would have liked to have had available while engaged in field work upon insect parasitology and the biological control of insect pests.”

Particular attention is given in the volume to those insects with a high degree of specialisation in their host relationship, and the generalised predators are dealt with more briefly and only sufficiently to illustrate the host preferences and habits of each group.

BOOK NOTICE.

The Biology and Control of Wireworms. Review of Literature. By C. A. THOMAS. (*Bull. Pennsylvania State College School Agric. Exper. Stat.* 392 : 1-90.) 8vo. 1940.

This Bulletin comprises the following chapters : Biology, Life history, and Ecology; Environment; Biological Control of Wireworms; Insecticides used against Elaterid Larvae; Attractants and Repellents; Planting Practices; Cultivation Practices; Crop Rotation; Miscellaneous Control Methods; Reviews of Literature on Wireworms; List of North American Investigators; Bibliography.

The work is intended for use in Pennsylvania in particular, but deals also with the problem of damage caused by the larvae of ELATERIDAE in the Temperate and Sub-tropical zones.

The work is, in a sense, a continuation of an earlier work by the same author published in 1930, and the literature reviewed is that published between 1930 and 1940.

“No attempt has been made to draw conclusions from this mass of information and the papers are summarised as nearly as possible in the form in which they were published.”

BOOK NOTICE.

The Parasites of man in temperate climates. By T. W. M. CAMERON. 8vo. Toronto (University of Toronto Press), 1940. Price \$3. pp. xi + 182, front., 60 figs.

This work is intended for the medical man practising in the temperate and sub-tropical zones of the earth. Only parasites which occur in North America or Great Britain are discussed in detail but such as may be introduced in patients returned from the tropics are discussed briefly.

The book is divided in sections as follows: Protozoa; Helminths; Leeches; Arthropods; Technique and a Bibliography and Index.

Each parasite is described and often the life-history is given. The effect of the parasite on man is described and the medical treatment for the destruction of the parasites and the restoration of health is given fully.

There is a short statement covering the medical aspects of Myiasis.

PUBLICATIONS

The Publications of the Royal Entomological Society are *Transactions* and *Proceedings*.

The *Transactions* form an annual volume, each paper in the volume being issued as a separate part. The parts are issued irregularly throughout the year.

The *Proceedings* are issued in three series:

Series A. General Entomology

Series B. Taxonomy

Series C. Journal of Meetings

Series A and B are issued in twelve parts, forming an annual volume of approximately 240 pages.

The following information is supplied for the guidance of authors wishing to submit papers for publication in any of the Society's journals.

INTRODUCTORY

The Society is prepared to undertake the provision of a reasonable number of text figures. The original drawings for such figures must be supplied by authors. Such drawings or groups of drawings must be drawn to a scale which will permit of their reduction to an area of dimensions not exceeding $7\frac{1}{4} \times 4\frac{3}{4}$ ". In the case of the *Proceedings Series A* and *Series B*, authors are required to pay for the necessary blocks for the provision of plates, half-tone and coloured work.

A uniform method is adopted for the citation of bibliographical references in the Society's publications as follows:

Smith, A., 1936, New species of Coccidae, *Proc. R. ent. Soc. Lond.* (B) 6 : 301-306, pl. 1.

—, 1936, New species of Coccidae, *Trans. R. ent. Soc. Lond.* 84 : 901-936.

Titles of periodicals cited are to be abbreviated in the manner indicated in the *World List of Scientific Periodicals*, 2nd edition, 1934.

Authors are entitled to receive 25 copies of their papers free of charge and may purchase additional copies provided that request be made before publication.

Papers offered for publication should be sent to the Secretary, Royal Entomological Society of London, at 41, *Queen's Gate, London, S.W.7*, and must be typewritten on one side of the paper only. Sufficient space must also be left between the lines for editorial corrections.

The copyright of the Society's publications is vested in the Society.

TRANSACTIONS

Papers offered for publication in the *Transactions* are considered by the Publication Committee of the Society, which meets usually in the months of May and November. In order that papers may be considered at these meetings it is necessary for the manuscript and drawings for any illustrations to be in the hands of the Secretary fourteen days before the meeting of the Committee.

Papers of less than eight printed pages (approximately 7000 words) will not normally be accepted for the *Transactions*, and papers by authors who are not Fellows of the Society must be communicated by a Fellow.

PROCEEDINGS SERIES A AND SERIES B

Papers submitted for publication in either *Series A* or *Series B* of the *Proceedings* by authors who are not Fellows of the Society may be accepted if they are communicated by a Fellow. Preference will be given to papers written in the English language, and papers of more than eight printed pages (7000 words) will not normally be accepted for publication in these journals.

PROCEEDINGS SERIES C

Series C is issued prior to every General Meeting. It contains abstracts of exhibits to be shown and communications to be made, together with the titles of papers accepted for publication.

The annual subscription to *Series A. General Entomology* is £1 4s. od.; *Series B. Taxonomy*, £1 4s. od. (single parts 3s. od.); and *Series C. Journals of Meetings*, 6s. od.

As from January 1936 the journal *Stylops* is continued as *Proceedings Series B. Taxonomy*. Copies of volumes 1-4 are available at £1 16s. od. each, post free.

MEETINGS
TO BE HELD IN THE SOCIETY'S ROOMS
41, Queen's Gate, S.W.7

1941.

WEDNESDAY, October	1
„ November	5
„ December	3

1942.

„ January	21	(ANNUAL MEETING)
„ February	4	

**THE ROYAL ENTOMOLOGICAL
SOCIETY OF LONDON**

The Fellowship and Fees

Fellows pay an Admission Fee of £3 3s. The Annual Contribution of £2 2s. is due on the first day of January in each year, and is payable in advance. Fellows under the age of 25 years may pay the entrance fee in three equal annual instalments.

Fees should be paid to the Treasurer, at 41, Queen's Gate, S.W.7, and *not to the Secretary.*

Fellows desiring to pay their Annual Contribution through their bankers may obtain an official form of banker's order by applying to the Treasurer.

Fellows whose Contributions for the current year have been paid are entitled to receive the *Transactions* and *Proceedings* of the Society free of charge. Further copies may be purchased at reduced prices by applying to the Registrar.

Forms of application for Fellowship, copies of the Bye-Laws and the List of Fellows may be obtained from the Registrar.

Meetings and Exhibitions

Fellows and others wishing to make a communication to a General Meeting of the Society are requested to send in their names, the title of their exhibit, and a short abstract of their remarks, to the Registrar fourteen days before the meeting at which it is proposed to make the communication. Should it be desirable to publish a fuller account of the communication the manuscript may be submitted for publication in *Proceedings Series A* or *Series B*. If the epidiascope is required, 24 hours' notice must be given. Objects for projection should not exceed 6 ins. by 6 ins.

Fellows resident abroad, or otherwise unable to attend meetings, are reminded that notes or observations sent to the Secretary may be communicated to a General Meeting on their behalf.